



Redescriptions and relationship of *Siphonaria zelandica* Quoy and Gaimard to *S. australis* Quoy and Gaimard with a description of *S. propria* sp. nov. (Mollusca: Pulmonata: Siphonariidae).

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ABSTRACT

Examination of the type material and anatomical features of several Australian and New Zealand species of the subgenus *Siphonaria*, previously considered distinct, indicates they are morphological forms of inadequately described species.

The synonymy and redescription of the external morphology, shell, reproductive system, spermatophore, radula and geographical variation of *S. zelandica* Quoy and Gaimard, 1833 and *S. australis* Quoy and Gaimard, 1833 is presented. A new name for *S. cookiana* Suter, 1909, necessary because the type series contains more than one species, is introduced with shell and anatomical descriptions. Comparisons are made with sympatric congeners. Shell and radular characters, originally used to describe species, are shown to be widely variable and considerably less useful than reproductive system features for species differentiation.

INTRODUCTION

While preparing a revision of the Siphonariidae it has become apparent that the identities of several Australian and New Zealand species of the subgenus *Siphonaria* Dall, 1870 are totally confused in the literature. Confusion between these species is due to inadequate original descriptions based on insufficient material and subsequent lack of referral back to the type material by later workers. To clarify the identities of these species, an examination of type specimens and redescription of reproductive systems, shell morphology and radulae with a subsequent comparison with sympatric congeners is presented.

Three species of the subgenus *Siphonaria*, *S. zelandica*, *S. australis* and *S. cookiana*, are generally recognized from New Zealand (Morton and Miller, 1968; Powell, 1979).

Quoy and Gaimard (1833) described *S. zelandica* and *S. australis* from New Zealand. *S. australis* was described, from only two specimens found, as occurring on the roots of an intertidal algae (presumably *Durvillea* holdfasts) in Cook Strait. The type locality of *S. zelandica* was generalized to New Zealand with the comment that Quoy and Gaimard believed it also occurred in Australia. Without reference to the type material, recent workers (Suter, 1913; Hubendick, 1946, 1955; Borland, 1950; Morton and Miller, 1968; Powell, 1979) have used these two names to separate high and low tidal forms of what is

shown in this paper to be one variable species. On examination of the types it appears that the stated type locality of *S. zelandica* is in fact incorrect. The syntypes are of a species commonly found in southern Australia but absent from New Zealand.

The third species, *S. cookiana* Suter, 1909, is also in taxonomic confusion. The species referred to by New Zealand workers as *S. cookiana* is indeed a distinct species but unfortunately Suter's type series contains more than one species. Subsequent designation of lectotype material (Boreham, 1959) has further confused the situation because the specimen she chose as the lectotype is in fact a juvenile of what is here considered *S. australis*, and so *S. cookiana* becomes a synonym of that name. The other six specimens of Suter's type series of *S. cookiana* are actually distinct from *S. zelandica* and *S. australis* and require a new species name.

S. inculta Gould, 1846 and *S. cancer* Reeve, 1856 are other names published for species of *Siphonaria* from New Zealand and, in this paper will be shown to be synonyms of *S. australis*.

MATERIALS AND METHODS

All of the material examined, except where noted, is in the collections of the Australian Museum (A.M.).

Anatomical features

The buccal mass, reproductive system and spermatophore were dissected from several specimens of each "species" preserved in 5% neutralized formalin. Animals with shells closely similar to those of primary type specimens provided anatomical comparisons of "species" originally described from only the shell. The radula was removed, by macerating the buccal mass in concentrated KOH for 24 hours, thoroughly washed in distilled water and stored in 70% alcohol. Radulae and spermatophore were either slide mounted and examined through a compound microscope or affixed to a microscope-slide cover slip fragment, mounted on a stub, coated with gold and examined under a scanning electron microscope (S.E.M.). Several specimens were examined from each sample lot to determine variation.

Definition of shell terminology (fig. 1)

The apex (a) is the dorsal extremity of the conically shaped shell consisting of a protoconch, which is generally broken off in all but very juvenile specimens. The shell lip (sl) fringes the ventrally located shell aperture. The curve of the anterior and posterior slopes of the apical sides may range from concave to convex. Primary ribs (pr) are apically continuous while the intermediate secondary ribs (sr) are narrower and apically discontinuous. Rib interstices (i) appear as furrows between ribs. The siphonal ribs, located on the right of the shell, are primary ribs and dorsally raised over the animals pneumostome. The spatula (s) is the interior apical area dorsal to the circularly arranged adductor muscle scars. The siphonal groove (sg) passes midway between the right anterior (arm) and right posterior (pam) adductor muscle scars. The siphonal angle (ϕ°) is the angle from the spatula between the inside edge of the left anterior adductor muscle scar (alm) and the siphonal groove. The curve of the cephalic muscle scar (cms), appearing as a thin line joining the anterior left and right adductor muscle scars, may range from concave to convex.

Shell characters

Caliper measurements of shell dimensions (i.e. length, width and height) were recorded from varying numbers of specimens throughout each species' distribution. The radial shell ribs on a line 1 cm to 1.5 cm in diameter from the shell apex were counted. The siphonal angle ϕ° was measured using a protractor. For each shell within samples from several geographical areas in the species' distribution, similar rib counts and shell measurements were recorded. Single shape dimensions and quotient ratios of length:width, width:height and length:height were used as measures of specific and geographical shell

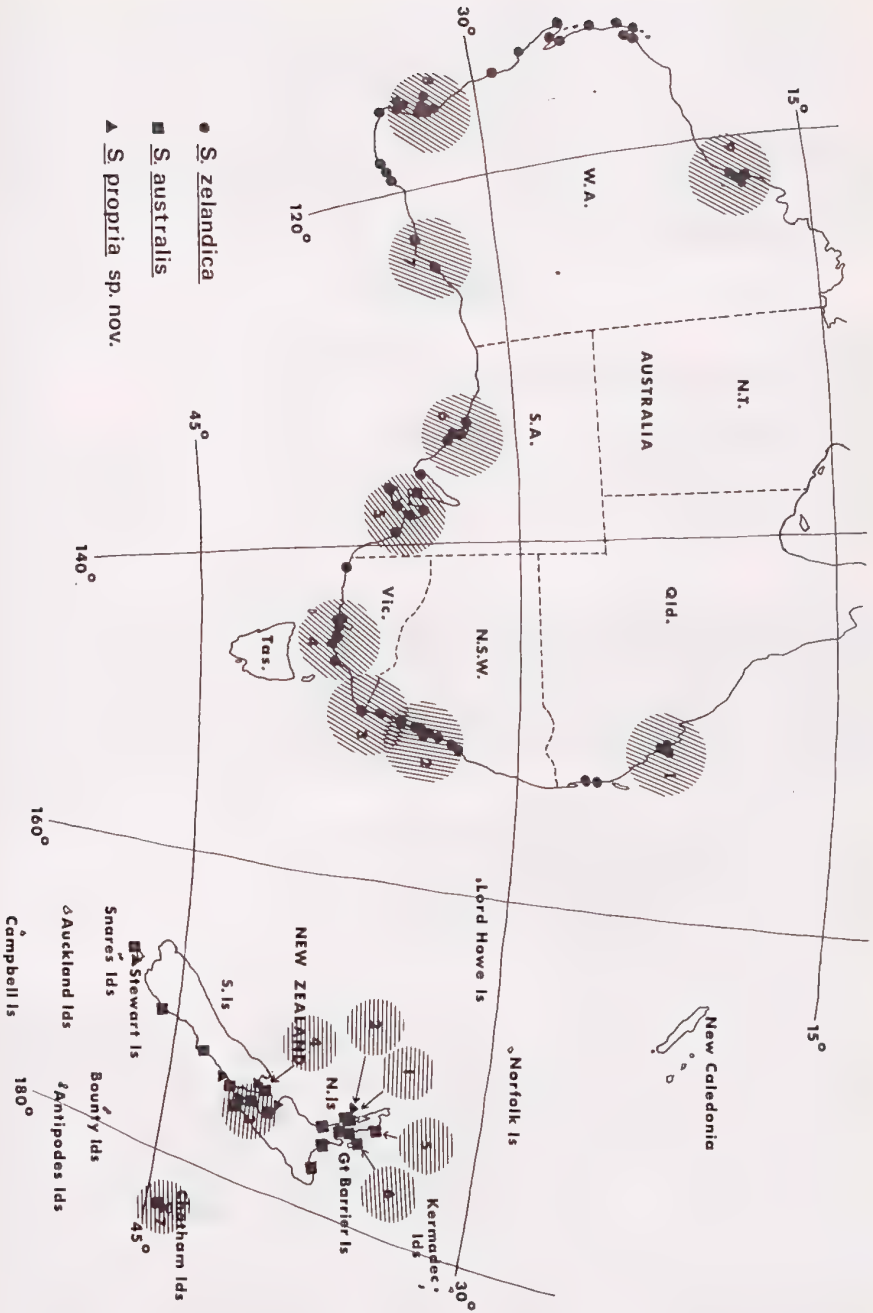


Fig. 1. The distributions of *S. zelandica*, *S. australis* and *S. propria* sp. nov. and dispersal of population samples (hatched areas) used to determine geographical shell variation.

variation. Specimens with an extremely eroded apex were not measured. The use of ratios in comparisons reduced the bias of sample age and/or locality exposure variation possibly existing within single shape variables. Variances of geographical samples were tested for homogeneity. Homoscedastic geographical data were subjected to a single classification analysis of variance (Sokal and Rohlf, 1969: 214) and where significant geographical variation existed a Student-Newman-Keuls test (Sokal and Rohlf, 1969: 240) provided an ordering of sample means. Heteroscedastic geographical data were subjected to a Kruskal-Wallis test of variance (Sokal and Rohlf, 1969: 288) and where significant differences existed a multiple comparison test of means (Sokal and Rohlf, 1969: 396) indicated an ordered relationship between samples. Critical values were from tables in Rohlf and Sokal (1969).

TAXONOMY

Family

Siphonariidae Gray, 1840 (sic. Siphonariadae). (non Adams, ?; — Suter, 1913)

Genus

Siphonaria Sowerby, January 1824 (non Blainville, November, 1824; — Hutton, 1882b)

Type

S. sipho Sowerby, January, 1824 (subsequent designation; Gray, MS, April, 1824 (non 1847; Powell, 1979: 292)).

Synonyms

Planesiphon Iredale, 1940. Type species (subsequent designation; McAlpine, 1952: 42)

Planesiphon elegans Iredale, 1940. *Ductosiphonaria*: — McAlpine, 1952: 42.

Planesiphon: — McAlpine, 1952: 42.

Subgenus

Siphonaria Dall, 1870, 31 (non Sowerby, 1824; auct.).

Synonyms

Simplisiphonaria Hubendick, 1945: 61

Siphonaria s. str. Hubendick, 1945: 61 (non Dall, 1870).

Ductosiphonaria Hubendick, 1945: 61

Simplisiphonaria: — Hubendick, 1946: 36; 1955: 5.

Ductosiphonaria: — Hubendick, 1946: 36; 1955: 4.

Planesiphon: — Hubendick, 1946: 20; 1955: 4.

Siphonaria s. str.: — Hubendick, 1946: 20; 1955: 6 (non Dall, 1870).

Taxonomic note on synonymy

According to article 42d of the International Code of Zoological Nomenclature (I.C.Z.N., London, 1966) "sectios" erected by Hubendick (1945) have subgeneric status. In addition, Hubendick's designation of type specimens for these generic subdivisions are unnecessary (article 64a). As shown in this paper many of Hubendick's subgeneric divisive criteria are based upon incorrect anatomical studies and misidentified type species. Species redescribed herein were placed into three different subgenera (= sectio) by Hubendick (1945; 1946): *S. cookiana* (by monotypy, *Simplisiphonaria*); *S. bifurcata* (type) and *S. baconi* (*Ductosiphonaria*); *S. australis*, *S. zelandica* and *S. elegans* (*Siphonaria* sensu stricto).

The above listed generic and subgeneric synonymies are incomplete. The genera and subgenera of the Siphonariidae will be reviewed in a forthcoming generic revision.

Siphonaria (*S.*) *zelandica* Quoy and Gaimard, 1833
(pls 1a — h, 2a — h)

Siphonaria zelandica Quoy and Gaimard, 1833: 344, pl. 25, figs 17, 18.
(sic. *zelandica*: auct.)

Siphonaria scutellum: — Hutton, 1878: 41 (non Deshayes, 1841).

Siphonaria zebra Reeve, 1856: species 21 (not 22), pl. 5, fig. 22.

Siphonaria baconi Reeve, 1856: species 30, pl. 6, figs 30, 30a.

Siphonaria baconi: — Angas, 1864: 189.

Siphonaria bifurcata: — Angas, 1867: 232; Hedley, 1918: M95; Iredale, 1924: 276
(non Reeve, 1856: species 21 (not 22), pl. 5, fig. 22).

Siphonaria zebra: — Hedley, 1918: M95; Hubendick, 1955: 4.

Siphonaria (*Ductosiphonaria*) *bifurcata*: — Hubendick, 1945: 22; 1946: 37, pl. 2, figs 9 — 13;
McAlpine, 1952: 42, fig. 3 (non Reeve, 1856).

Planesiphon elegans Iredale, 1940: 441, pl. 34, figs 3,4.

Siphonaria (*Ductosiphonaria*) *baconi*: — Hubendick, 1946: 37, pl. 6, figs, 10, 11.

Ductosiphonaria elegans: — McAlpine, 1952: 42

Planesiphon elegans: — Hubendick, 1955: 4.

Siphonaria (*Planesiphon*) *zelandica*: — Hubendick, 1955: 4, pl. 1, figs 5 — 8.

Types

S. zelandica: (herein designated) Lectotype (tallest syntype, has the clearest external sculpture); Paralectotypes (2), Museum National d'Histoire Naturelle, Paris (M.N.H.M.).

Type Locality

New Zealand (erroneous; undoubtedly from Australia).

Description of Lectotype (pl. 1a)

Shell height less than 1/3 shell length; apex nearly central; apical sides straight to weakly convex; exterior uneven and apex eroded; growth ribbing indistinct; approximately 17 slightly raised, broad and abapically straight white primary ribs; siphonal ribs not prominent; 2-3 thin secondary ribs occur between primary ribs; the shallow, white rib interstices are flecked with brown; interior smooth; cephalic muscle scar is straight to weakly concave; spatula and shallow siphonal groove tan to yellow; shell margin thickened and white mottled with brown; shell lip white with irregular brown rays aligned under exterior rib interstices.

Dimensions

	length mm	width mm	height mm
Lectotype	20.8	19.0	5.3 (pl. 1a)
Paralectotypes	21.0	17.9	5.2
(2)	18.2	15.4	4.3
original description	20.3	18.0	9.0
original figure	20.2	18.2	— (dorsal)

Remarks

The shell height in the original description is incorrect.

Additional material examined (preserved (p) and dry (d))

Qld.: Keppel Is. (6d); Emu Park, Keppel Bay (2d); S. Keppel Is. (3d); Keppel Bay (1d); Bargara (4p); Noosa Hd (15+p); Caloundra (10d); N.S.W.: Bateau Bay, The Entrance (6d); Blue Lagoon Bch, S. of Tuggerah Lakes (10d); Toowoomb (7d); Kilcare Bch (2p); Ettalong Bch, Broken Bay (2d); Syd.; Palm Bch (1d), Long Reef (15+d), Freshwater Bch, Manly (12d), Port Jackson (11d), Middle Hd (10d), Clontarf (15+d), Balmoral (7d), Bronte (15+d), Maroubra (1d); Sussex Inlet, S. coast (11d); Twofold Bay (1d); Vic.; Mallacoota (13d); Balnaring (4d); Cheviot Bay (1d); Western Port (10d); Blowhole, near Flinders (3d);

Flinders (15+p); Cape Schank (15+p); Portsea (15+p; 4d); Queenscliffe, Port Phillip (14p); Pt Lonsdale (5p); S.A.; Robe (2d); Glenelg Bch (5d); Kangaroo Is.; (7p; 6d), Nepean Bay (2p), Red Bank, Nepean Bay (4p), Emu Bay (1p); Normanville (1p; 2d); Marino Rocks, St Vincents Gulf (12d); Corny Pt (10d); Tumby Bay (13d); Ceduna (8d); Aldinga (5p); Streaky Bay (15+p; 15+d); Pt Sinclair (7d); W.A.; Esperance (1d); S. Point, Two Peoples Bay (1d); Middleton Beach, King George Sound (2d); Margaret River (15+d); S. of Cowaramup (9d); S. Cowaramup (3d); Wyadup (1p); Canal Rocks, near Yallingup (4p); Kilcarnup (1d); Dunsborough (2p); Geographe Bay (8d); Garden Is. (15+d); Pt Peron (10p; 3d); Rottnest Is.; Thomson Bay (7p; 2d), Radar Reef (15+p), Strickland Bay (4p); Fremantle (13d); Port Denison, Dongara (1d); Abrolhos Ids (3p; 1d); Horrocks Bch, N. of Geraldton (15+p); Pt Cloates (3d); Dirk Hartog Is. (1d); Quoin Bluff, Dirk Hartog Is. (1d); Denham (6d); Monkey Mia, E. side of Peron Peninsula (2d); Pt Quobba (5p; 1d); Coral Bay, S. of Exmouth Gulf (2p); N.W. Cape (3p); Broome; (8d), Cable Bch (4d), Gantheaume Bay (1d): total (206+p; 363+d).

DISTRIBUTION

S. zelandica is restricted to a southern distribution around the eastern, southern and north-western coasts of Australia (fig. 2). Its northern limits on the eastern and north-western coasts appear to be Keppel Bay, Qld. (23°25'S, 150°55'E), and Broome, W.A. (17°58'S, 122°14'E) respectively. No records of this species are known from Tasmania. *S. zelandica* commonly occurs on exposed rocky intertidal shores between the mid and supralittoral zones, often on horizontal rock facings, in shallow pools or around regularly saturated algal mats.

DESCRIPTION

External morphology (live specimens)

The sole of the foot and visceral mass of the animal are a pale green-grey. The side of the foot mantle and head region are cream with a lighter fringe on the foot edge. Under the right-hand side mantle edge a broad, translucent, white fold covers the posteriorly offset pneumostome. The mantle is broad fringed by a thick edge with a continuous white subepithelial band. Yellow subepithelial mucous cells are uniformly dispersed over the external tissues (except on the sole of the foot) becoming more vivid and densely concentrated around the pneumostomal fold and cephalic lobes. Both the head and the right anteriorly opening genital pore are inconspicuous. Two small black subepithelial eye spots are centrally located on two cream, thick cephalic lobes. These lobes touch and extend over the mouth region. The side of the foot often appears swollen. The internal cuticular covering the visceral mass is shaded black apart from an area covering the mantle cavity.

Shell (figs 1A, B, C; pls 1, 2)

length mm $\bar{x}$ = 15.1, s = 2.6, n = 180

width mm $\bar{x}$ = 12.2, s = 2.7, n = 180

height mm $\bar{x}$ = 4.2, s = 0.9, n = 180

The shell is asymmetrical and thin with slightly raised and usually broad primary radial ribbing. The exterior is often eroded or overgrown with *Lithothamnion* or other microphytic algae. The apex is offset to the left and posterior, the height of which is usually less than a third of the shell length. Slightly raised, mainly broad, apically continuous, white primary ribs (prim. ribs/shell $\bar{x}$ = 17.6, s = 2.5, n = 180) radiate from the apex with black to light brown interstices finely striated with four to six apically discontinuous secondary ribs. Growth striae are fine to inconspicuous. The apical sides of the shell are straight to concave. The outer lip is uneven, often broken, and finely scalloped with primary ribs extending past the outer lip. From the exterior the siphonal groove is indistinct. The pneumostomal margin of the shell is slightly raised and the outer edge extends weakly out to the right side. The interior is smooth with brown to white spatula and a slightly swollen margin. Brown apical rays are often presented extending from the spatula to the slightly swollen lip margin corresponding with exterior rib interstices. The siphonal groove (fig.

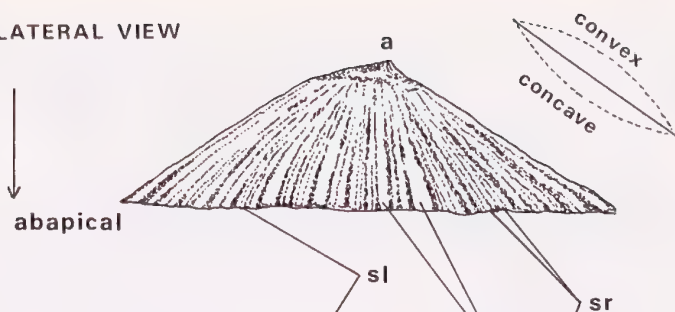
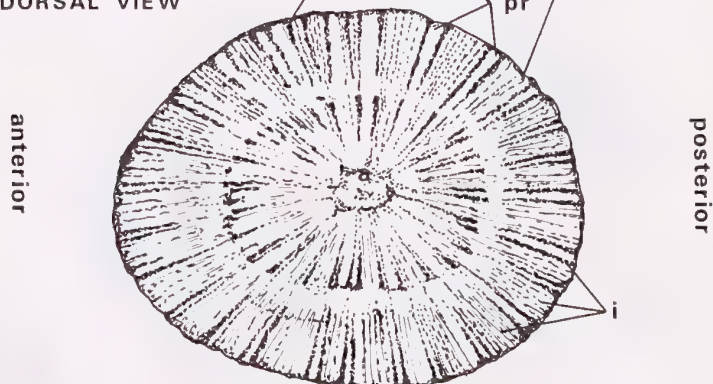
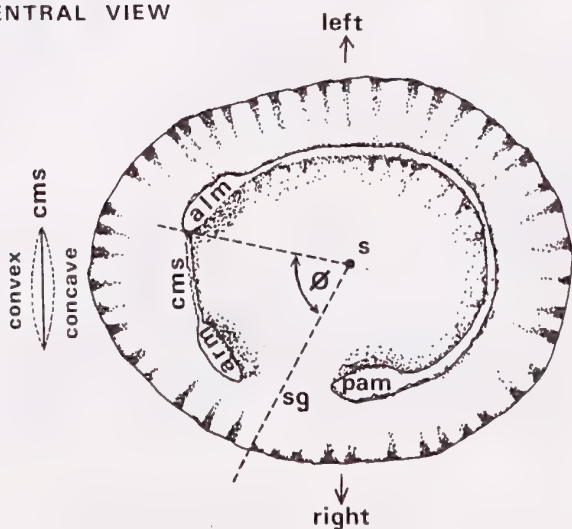
A LATERAL VIEW**B DORSAL VIEW****C VENTRAL VIEW**

Fig. 2. Schematic representation of shell terminology. a — apex, alm — left adductor muscle scar, arm — right adductor muscle scar, cms — cephalic muscle scar, i — rib interstices, pam — posterior adductor muscle scar, pr — primary ribs, s — spatula, sl — shell lip, sm — shell margin, sr — secondary ribs, sg — siphonal groove, $\circ^\circ$ — siphonal angle.

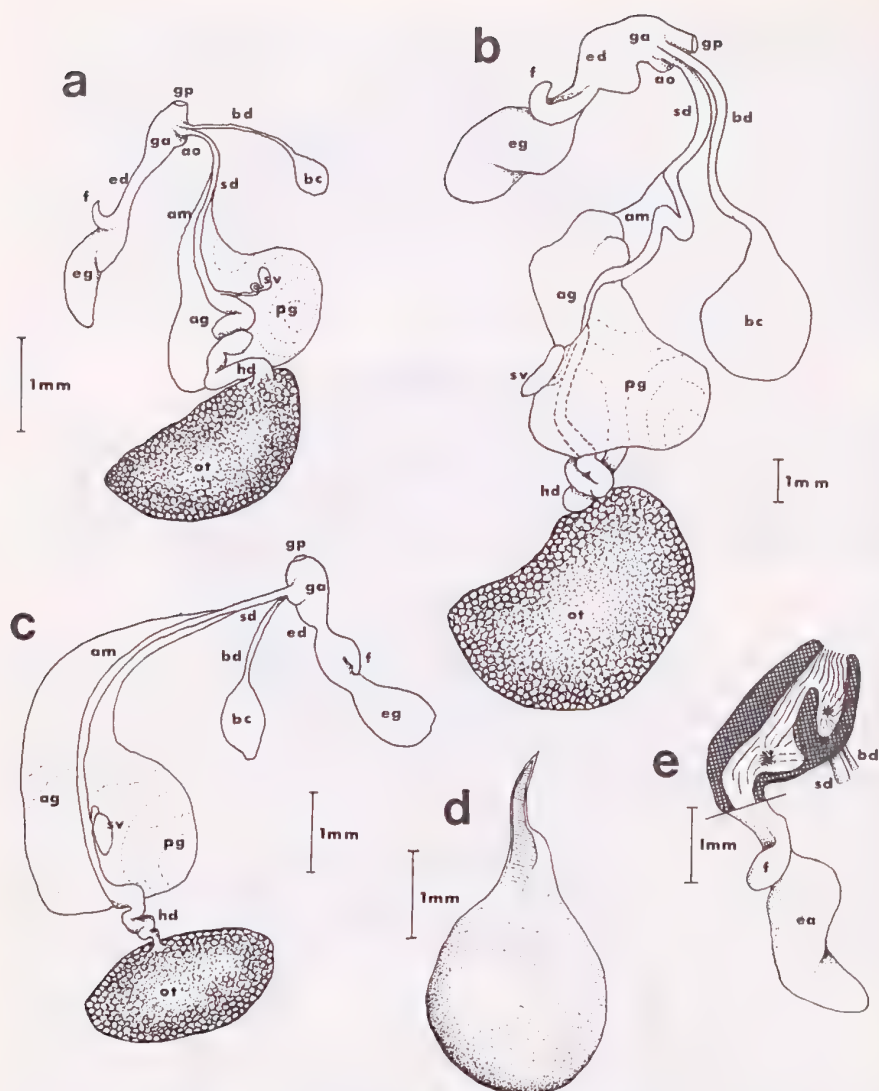


Fig. 3. Reproductive systems and spermatophore of *S. zelandica*. a) Streaky Bay, S. A. (pl.2d), dorsal view; b) Shelly Beach, rock platform, Caloundra, Qld. (pl.2a), dorsal view; c) Radar Reef, Rottnest Is., W. A. (pl.1e), ventral view; d) spermatophore, Shelly Beach, Caloundra, Qld. (pl.2a); e) longitudinal section of epiphallus duct and genital atrium, Portsea, Vic.

1C; sg) is shallow, smooth, of a similar colouration to the spatula and at an angle of 75° (ϕ°) to the right anterior adductor muscle scar. The cephalic muscle scar (fig. 1C, cms) is shallow and weakly concave to straight. The adductor muscle scars are similarly shallow and may be a darker or lighter brown than the spatula. Juvenile shells, usually distinguished by size, generally have similar ribbing with a paler interior and exterior than adult specimens.

Reproductive system (figs 3a, b, c)

The yellow, granular ovotestis (hermaphrodite gland; ot) fills the posterior region of the coelom. Closely joined to the ovotestis via thin branching ducts is the thick, lobed and coiled, brown coated, yellow hermaphrodite duct (hd). The pinkish yellow, bulbous seminal vesicle (sv) is joined by a very thin translucent duct to the junction of the hermaphrodite duct and white spermoviduct (sd). The large, white, folded posterior mucous gland (pm) and albumen gland (ag) complex, are anterior to the ovotestis and envelope the seminal vesicle. A white, folded anterior mucous gland (am) surrounds the anterior portion of the spermoviduct with decreasing thickness from the hermaphrodite duct to the anterior adductor muscle. A narrow, elongated, flat, white prostate gland extends along the right dorsal surface of this spermoviduct. The thick, muscular, cream epiphallus duct (ed) and lobed, cream coloured gland (eg) are situated between the anterior adductor muscle and the buccal mass. The duct is wide and often twisted. The gland is longer than the duct, flattened and partially split by a central fold. A short "spur" like flagellum (f) occurs as an extension of the duct junction with the gland. The muscular genital atrium appears as a swollen extension of the epiphallus duct (ed) with a small weakly protruding accessory atrium. The genital pore (gp) opens exteriorly through the foot wall under the mantle between the right-hand side cephalic fold and pneumostomal lobe. The brown, spherical bursa copulatrix (bc) enters the genital atrium (ga) through a long, thin, white bursal duct (bd) more towards the genital pore than the spermoviduct opening. The juxtaposed bursal and spermoviducts (bd ventral to the sd) respectively enter the genital atrium and accessory atrium with the spermoviduct passing through epiphallus duct tissue to enter higher and separate to the bursal duct (fig. 3c). Both ducts pass through the right-hand side of the anterior adductor muscle before entering the genital atrium. The white lumen (l) of this atrium and of the accessory atrium is muscular with large longitudinal internal tissue folds. The bursa cuticle, when holding a spermatophore, stretches taking the spermatophore's shape (fig. 3b). After the spermatophore has been discharged the bursa diminishes in size and the cuticle, appearing deflated and withered, hardens around a small amount of brown reproductive waste products (fig. 3a, c). The reproductive systems of *S. zelandica* figured in McAlpine (1952: 43, fig. 3 "*bifurcata*") and Hubendick (1955: 10) are schematic, not detailing glands or duct openings.

Spermatophore (fig. 3d)

The spermatophore is "droplet" shaped with a bulbous head. The short, thick, pointed, pink spermatophore tail extends into the top sections of the spermathecal duct. The tail is less than a quarter of the total spermatophore length. A thin, transparent test surrounds the spermatophore. Within the test of the tail a broad, white core is centrally aligned and longitudinally compressed along the length of the tail. The core colour changes to pink where it extends for a short distance into the head along one side between the test and the yellow head matrix. For an animal 17.5 mm in length the spermatophore was 4 mm long and 2 mm wide.

Radula (pl. 6a, b, c)

Wide intraspecific variation exists in the number of transverse rows and the number of inner, mid and outer lateral teeth in longitudinal rows. The mean dentition formulae is 28:1:28 ($s = 3.8$, $n = 7$) with 122 parallel and slightly curved (anteriorly convex) transverse rows ($s = 6.5$, $n = 8$). Of the 28 half row laterals, 10 ($s = 2.4$) and inner, 2 ($s = 0.8$) mid and 16 ($s = 1.5$) outer teeth means respectively ($n = 8$). In each longitudinal row a gradual reduction in tooth size and an increase in distance between transverse rows occurs from the central tooth to the outer laterals. All teeth are bluntly concave posteriorly. The central tooth has a lower profile than the flanking laterals and a short pointed mesocone less than half the

base length. The anterior is forked and wider than the notched posterior. The narrow base interlocks and articulates with the adjacent central teeth. Lateral teeth have broad bases. The mesocone of the inner laterals is either pointed or bicuspidate. The inner cusp is always longer and usually overlapping the posterior of the inner lateral in front. Ecto and endocones are absent. The mid laterals have an ectocone and a bluntly bicuspidate mesocone with the inner cusp being the longer. Outer laterals have a square shaped base with a broad blunt mesocone flanked by short pointed ecto and endocones. The clefts between the mesocones and the side denticles of the outer laterals are widely variable in width and angle of separation. Around the third or fourth outer longitudinal row, often aberrant outer lateral teeth appear as fused teeth with double mesocones.

Geographical variation

Apart from slight variations between individuals, no geographical variation was evident in size, shape and pigmentation of reproductive organs or external morphology of specimens from different regions.

Differences in shell morphology were found to occur between the 9 population samples (table 1a). Apart from the length : width ratio, differences between samples in shell length, width ($p < 0.001$), height, length : height ratio and number of ribs ($p < 0.002$) were all highly significant with the shell length : width : height ratio of a lower significance ($0.01 > p > 0.001$) (table 2). Comparative ordering of population samples indicated the northern most samples from eastern and north-western coasts of Australia (i.e. South of Keppel Bay and Broome respectively) were similar in shell morphology. Most heterogeneous partitions (0.05 prob. level) occurred between southern Western Australia and western South Australia, and eastern South Australia and western Victoria (table 2). A clinal decrease in overall shell size is apparent from the northern to south-western populations. The shell form of southern populations is generally smaller in length, width and height but proportionally similar to other more northern populations. The sample from south-eastern Western Australia has significantly fewer primary ribs ($p < 0.002$) than all other population samples which exhibit little intersample variation. Shell colouration of the southern form, particularly of the internal surface (pl. 2b-e) is paler than the more northern forms which often have broad dark brown radial banding mainly on the lip margin (pls 1f-h, 2a, f, g).

DESCRIPTION OF SYNONYM TYPE MATERIAL

The type material of other species previously considered distinct, now considered synonyms of *S. zelandica*, are listed below.

Siphonaria baconi Reeve, 1856: species 30, pl. 6, figs 30a, b.

Types

(Herein designated) Lectotype (tallest syntype, has the darkest internal apical rays) British Museum (Natural History) (B.M. (N.H.)) 1979164; Paralectotypes (2) B.M. (N.H.) 1979164.

Type Locality

Swan River, Western Australia.

Description of Lectotype (pl. 1b)

Shell height less than 1/3 shell length; apical sides weakly convex; apex central and eroded; shell thin and conically flat; growth ribbing indistinct; about 17 weakly raised, narrow, and abapically straight white primary ribs; siphonal ribs not prominent; 3-6 thin secondary ribs occur between primary ribs; rib interstices white and mottled with dark brown flecks; interior smooth; cephalic muscle scar straight to weakly concave; spatula and shallow siphonal groove yellowish tan; shell margin thickened and cream to white with irregular pale brown rays extending and broadening over the white shell lip; adductor muscle scar shallow and cream to tan.

Dimensions

	length mm	width mm	height mm
Lectotype	22.7	18.8	5.3 (pl. 1b)
Paralectotypes	24.4	20.3	4.9
	23.1	18.7	4.6 (pl. 1c)
original figure	24.1	19.5	—

Siphonaria zebra Reeve, 1856: species 22 (not 21), pl. 5, fig. 21.

Types

(Herein designated) Lectotype (longest syntype) B.M. (N.H.) 1979168. Paralectotypes (3) B.M. (N.H.) 1979168.

Type Locality

Port Jackson on type label; Philippines in Conch. Icon. (incorrect).

Description of Lectotype (pl. 1e).

Shell height less than $\frac{1}{4}$ shell length; apex subcentral, eroded; exterior slightly uneven; posterior half of shell slightly wider than anterior; growth lines are indistinct; approximately 21 broad, weakly raised, and abapically straight white primary ribs; siphonal ribs are not prominent; 2-3 thin secondary ribs occur between primary ribs; the shallow rib interstices fade adapically from dark brown to white with brown flecks; anterior smooth; adductor muscle scars prominent; cephalic muscle scar is weakly concave; spatula is dark yellowish tan; shell margin is thickened and similar to the shell lip is white with broad brown rays corresponding to exterior rib interstices.

Dimensions

	length mm	width mm	height mm
Lectotype	25.8	21.2	6.1 (pl. 1e)
Paralectotypes	21.3	17.8	5.3 (pl. 1f)
(3)	24.4	17.6	5.8 (pl. 1g)
	18.6	16.5	4.9 (pl. 1h)

Planesiphon elegans Iredale, 1940: 441, pl. 34, figs 3, 4.

Types

Holotype A.M. C.103710. Paratypes (11); A.M. C.126707, (6) A.M. C.108528.

Type Locality

North Keppel Is. and Emu Park, Keppel Bay, Queensland.

Description of Holotype (pl. 1d)

Shell height less than $\frac{1}{3}$ shell length; exterior conically flat; apex subcentral and eroded; apical sides weakly convex; growth ribbing indistinct; approximately 18 narrow, weakly raised and abapically straight white primary ribs; siphonal ribs are not prominent, 4-6 thin secondary ribs are present between primary ribs; the very shallow rib interstices are thin; interior smooth; cephalic muscle scar straight to weakly convex; spatula yellow to tan; shell margin white and thickened; shell lip white with brown rays corresponding to exterior rib interstices; adductor muscle scars shallow and yellowish tan.

Dimensions

	length mm	width mm	height mm
Holotype	19.5	15.3	5.0 (pl. 1d)
Paratypes (11) $\bar{x}$	17.3	13.9	4.0
s	4.3	3.8	1.2

Siphonaria (*S.*) *australis* Quoy and Gaimard, 1833
(pls 3a-e, h, i; 4a-g)

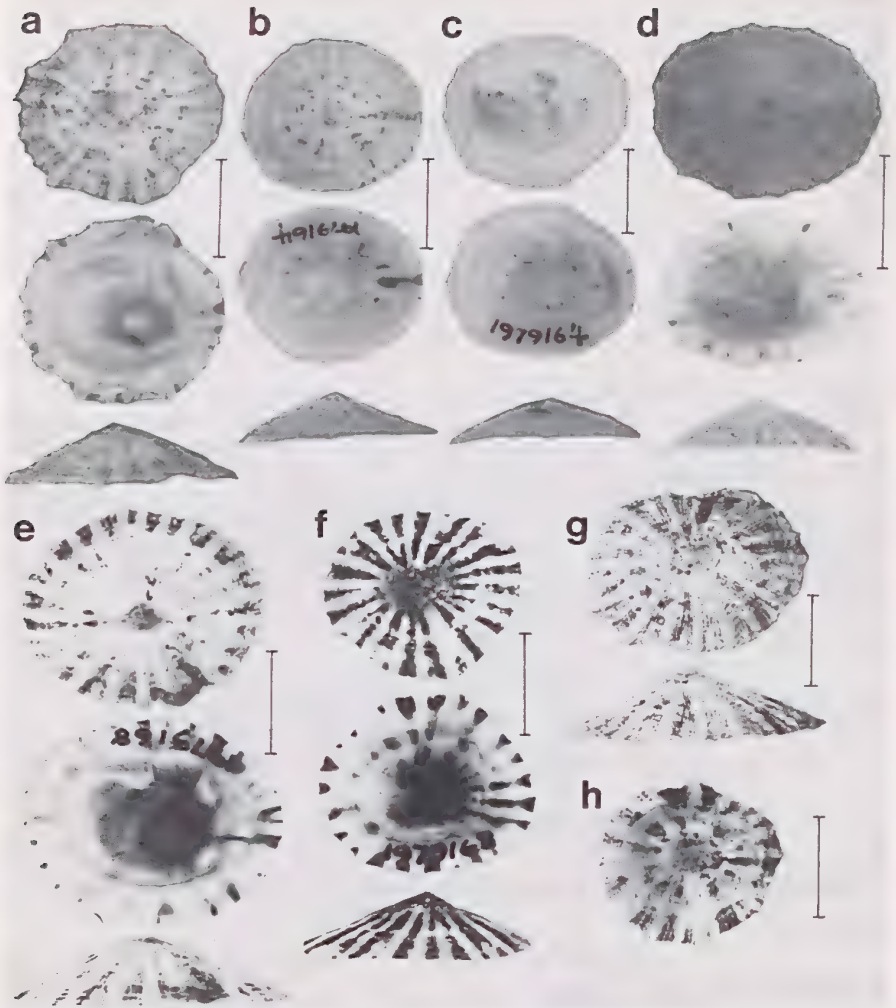


Plate 1. *Siphonaria zelandica*; a) lectotype (herein designated); b) *S. baconi* lectotype (herein designated) Swan River, W. A.; c) *S. baconi* paralectotype; d) *P. elegans* holotype, Keppel Bay, Qld.; e) *S. zebra* lectotype (herein designated) Port Jackson, N.S.W.; g-i) *S. zebra* paralectotypes.

Siphonaria australis Quoy and Gaimard, 1833: 329, pl. 25, figs 32-34.

Siphonaria radiata Blainville, 1827: 294 nomen dubium (non Sowerby, 1835:6 non Adams and Reeve, 1850: 69, pl. 8, figs 2a, b.)

Siphonaria costata Hombron and Jacquinot, 1841: 192 nomen nudum (non Sowerby, 1835: 6).

Siphonaria inculta Gould, 1846: 153, pl. 30, fig. 464.

Siphonaria cancer Reeve, 1856: species 7, pl. 2, figs 7a, b.

Siphonaria siphon — Reeve, 1856: species 9; Hutton, 1880: 36 (non Sowerby, 1824).

Siphonaria australis: — Hutton, 1878: 42; 1880: 36; 1882a; 1882b: 142, pl. 17, figs E — G; Moss, 1908: 41, pl. 9, fig 25; Suter, 1913: 598, pl. 24, fig. 6; Bucknill, 1924: 82; Powell, 1939: 217; 1946: 91; 1957: 114; 1979: 292, pl. 54, fig. 11; Borland, 1950: 390; Knox, 1955: 86; Morton and Miller, 1968: 302, pl. 19, figs 7, 7a.

Siphonaria zelandica: — Hutton, 1878: 41; Suter, 1913: 600, pl. 24, fig. 8 (shell); Iredale, 1915: 478; Bucknill, 1924: 82, pl. 3, figs 16, 16a; Powell, 1939: 217; 1946: 91; 1957: 114; 1979: 292, pl. 54, fig. 10; Borland, 1950: 386; Knox, 1955: 86; Morton and Miller, 1968: 269, 302, pl. 19, figs 8, 8a (non Quoy and Gaimard, 1833).

Siphonaria inculta: — Hutton, 1878: 7; Suter, 1913: 600.

Siphonaria cancer: — Hutton, 1880, 36.

Siphonaria cookiana Suter, 1909: 258 (in part).

Siphonaria cookiana: — Suter, 1913: 599, pl. 24, figs 7, 7a, 7b; Boreham, 1959: 71 (lectotype).

Kerguelenia australis: — Iredale, 1915: 478.

Siphonaria (Simplisiphonaria) cookiana: Hubendick, 1945: 20, figs 21, 24, 26; 1946: 36, pl. 6, figs 20-22 (non Suter, 1909).

Siphonaria (Siphonaria) australis: — Hubendick, 1946: 49, pl. 3, figs 28 — 31; 1955: 7 (in part).

Types

S. australis: (herein designated) Lectotype (larger syntype); Paralectotype (1), M.N.H.N.

Type Locality

Cook Strait, New Zealand.

Description of Lectotype (p1. 3a)

Shell height less than 1/3 shell length; apex posteriorly offset to the left; exterior uneven and tan; approximately 30 evenly spaced, pale brown radial ribs; concentric growth lines fairly distinct; apical sides strongly convex; siphonal ribs raised but not prominent; interior glossy; spatula and shell siphonal groove tan and mottled with brown; adductor muscle scars pale brown; cephalic muscle scar weakly convex; shell margin smooth and tan; shell lip tan with white rays corresponding to exterior ribbing.

Dimensions

	length mm	width mm	height mm
Lectotype	16.2	11.3	5.1 (pl. 3a)
Paralectotype	12.5	8.9	4.3
original description	15.8	11.3	6.8

Additional material examined (preserved (p) and dry (d))

New Zealand; (6d); North Is.; E. Coast, Akau, near Whangamumu (15+d); Whangarei, Suter colln, New Zealand Geological Survey (N.Z.G.S.) (5d); Great Barrier Is. (1d); Whangaparaoa; (15+p), Papa Rock, Tindalo Bch (15+p, 3d), Stanmore Bay (15+p, 2d); Onetangi, Waiheke Is., Hauraki Gulf (3d); Takapuna, N.E. of Auckland (6d) (N.Z.G.S.) (2d); Katikati (4d); near Motu River, Bay of Plenty (7d); W. coast, Motutara (11d) (N.Z.G.S.) (11d); Auckland; Kare Kare, N. coast (15+p, 3d), Deep Ck, N. of Auckland (N.Z.G.S.) (8d). Manukau Harbour (5d), (N.Z.G.S.) (6d), Kakamatus, Manukau Harbour (15+p, 2d); Port Waikato (2d); Wanganui Heads (1d); ocean reef, Pipikariti (12d); Kapiti Is. (N.Z.G.S.) (6d); Wellington (1d); Pt. Howard, Wellington Harbour (N.Z.G.S.) (1d); Lyall Bay (N.Z.G.S.) (10d); Cook Strait (6d), South Is.; Fossil Pt, N. of Nelson (N.M.N.Z.) (15+p, 3d); E. coast, S.

side of Kaikoura Peninsula (2p, 1d); Lyttelton, Suter colln. (N.Z.G.S.) (7d); New Brighton; in roots of *Durvillea*, Suter colln. (N.Z.G.S.) (7d), near Christchurch (3d); Hatchery Bch, Portobello, near Dunedin (4d); Kakarui, Otago (N.Z.G.S.) (5d); North Arm, Port Peggusus, Stewart Is. (N.M.N.Z.) (1p, 1d); Station Pt, Snares Ids, On *Durvillea* (1p); Chatham Ids; Suter colln. (N.Z.G.S.) (15+d); Glory Bay, Pitt Is. (N.M.N.Z.) (12p, 2d), Waitangi, (N.Z.G.S.) (7d); Auckland Is, Suter colln. (N.Z.G.S.) (1d); total (106+p, 185d).

DISTRIBUTION

S. australis occurs on exposed and semi-exposed rocky intertidal shores throughout the New Zealand, Chatham, Stewart, Auckland and Snares Islands (between the latitudes of 34° and 48°S (fig 2)). It is not recorded from the Kermadec (Oliver, 1915), Bounty or Antipodes (Powell, 1979) Islands. This species appears to have a wide vertical intertidal distribution being associated with the zone indicators *Durvillea antarctica*, *Hormosira banksii*, *Corallina officinalis* and *Lichina pygmaea* var *intermedia*. Originally described from two specimens as occurring "on" the roots of apparently *D. antarctica* the nominal form of *S. australis* has also been recorded "under" and "in" the holdfasts of *D. antarctica* (Suter, 1913; Hubendick, 1946; Borland, 1950) and "on rocks" (Hutton, 1882a), while the *S. "zelandica"* form inhabits rock surfaces (Hubendick, 1946; Borland 1950; Morton and Miller, 1968; Powell, 1979). Several collectors, who provided preserved material for this work, were unable to find siphonariids on kelp holdfasts. Only one available preserved specimen collected from *Durvillea* holdfasts (Station Pt, Snares Ids, coll: G. Fenwick, Dec. 1976) was examined. While this specimen's extremely flattened shell form (pl. 4f, lateral) differs from *S. australis* (pls. 3, 4), its shell colouration (pl. 4f, ventral), radula (pl. 6d) and reproductive system (fig. 4b) indicate it is conspecific.

Morton and Miller (1968) and Powell (1979), after Borland (1950), considered *S. "australis"* to occupy low shore zones and the larger *S. "zelandica"* the mid and upper zones. Specific differentiation by these authors was apparently solely on shell form without anatomical considerations.

DESCRIPTION

External morphology (preserved animals)

The smooth sole of the foot and fringe are white to cream, while, the smooth side of the foot is mottled black with large, irregular, circular white spots with centralized pustules, where subepithelial mucous cells open. No black colouration occurs under the cephalic lobes on the side of the foot. The mantle is narrow, thin, grey to black with the lobed and swollen outer mantle edge banded with black radial lines corresponding with shell rib interstices, but broken by white areas aligned with shell ribs. The pneumostomal fold is long, white and lightly shaded with black. Two indistinct, black, subepithelial eye spots are laterally offcentred on the two, large, thick, white, centrally touching cephalic lobes. The cuticle above the cephalic lobes and over the head area is shaded black. This shading appears stippled on the lobes. The internal cuticle covering the visceral mass is stipple shaded black over the head, siphonal duct and mantle cavity, decreasing in density over the posteriorly situated hermaphrodite gland.

Shell (pls 3a-e, h, i, 4a-g)

length mm $\bar{x}$ = 17.99, s = 1.93, n = 99

width mm $\bar{x}$ = 13.6, s = 3.04, n = 99

height mm $\bar{x}$ = 6.24, s = 1.82, n = 99

The shell of this species is extremely variable in size and colouration. Generally it is ovate, asymmetrical and thick with broad, raised and irregularly spaced radial ribs. The grey-light brown exterior is usually eroded or overgrown with algae or *Chamaesipho* barnacles. The apex is offset to the left posterior and when not eroded has an apical notch (protoconch). The apical sides are convex (fig. 1A), particularly close to the shell margin. This convexity is accentuated at the posterior margin. Growth ribbing is indistinct and may appear as discontinuities in shell formation. The external sculpture is widely variable. The radial ribs ($\bar{x}$ = 28.5, s = 4.4, n = 99) project past the shell margin with the two prominent

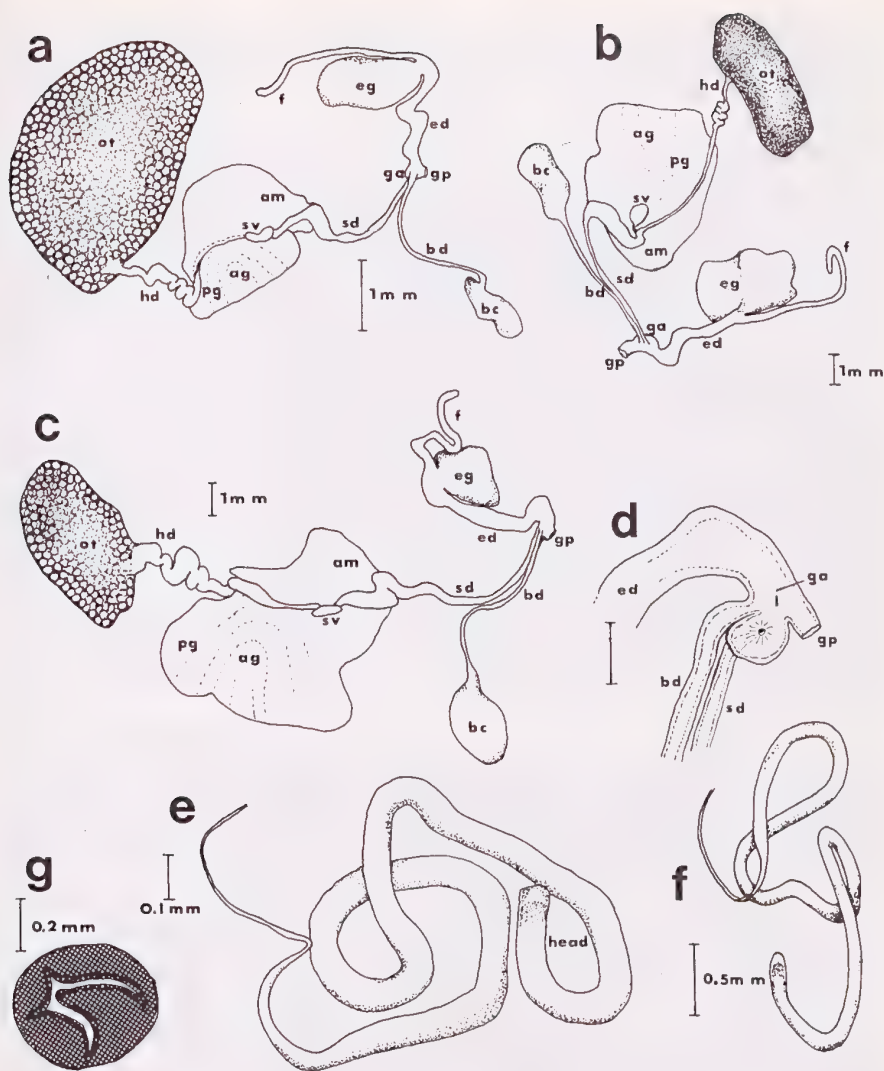


Fig. 4. Reproductive systems and spermatophore of *S. australis*. a) Fossil Pt., N. Nelson, N.Z., dorsal view; b) Station Pt., Snares Ids, N.Z., dorsal view; c) Glory Bay, Pitt Is., Chatham Ids, N.Z. dorsal view; d) longitudinal section of genital atrium; e) spermatophore of c; f) spermatophore of b; g) transverse section of epiphallus duct, Kakamatua, Manukau Harbour, N.Z.

juxtaposed siphonal ribs projecting the furthest. The radial ribbing on the left of the shell is usually finer with narrower interstices. Rib interstices appear as dark brown furrows which bifurcate as inverted "V" shaped markings where secondary ribs develop in the cleft (pl. 3d, e, h). Interstices of some large specimens develop into deep grooves (pl. 3c, d). The shell interior is glossy and uneven. The blue and yellowish tan spatula and siphonal groove are usually mottled with dark brown or grey. In the shallow adductor muscle scars and immediately below the spatula, the interior shell colouration is light brown to tan, while

the lip margin, below the muscle scars, is chocolate brown with white rays tipping the underside of the ribs. The cephalic muscle scar (fig. 1C; cms) is slightly convex. The siphonal angle ϕ° is $x = 77^\circ$ ($s = 3.18$, $n = 18$). Juvenile shells usually have flat, light brown ribs with a chocolate brown spatula and shell interior.

Reproductive system (fig. 4a-c)

The epiphallus gland (eg) and duct (ed) are positioned in the coelom between the buccal mass and the right anterior adductor muscle, immediately below the thin cuticle covering the visceral mass. In the right posterior side of the coelom, the ovotestis, mucous and albumen glands are situated under the digestive gland and dorsal branchial cavity. The genital pore (gp) is small, opening through the foot wall posterior to the right cephalic fold. The yellow, granular ovotestis (ot), unlike the other major reproductive glands and ducts, slightly varies in proportional size between individuals. From the ovotestis several very small, thin, translucent ducts join to form the swollen, pinkish cream, unlobed hermaphrodite duct (hd). The weakly folded duct narrows and straightens as it is enveloped by the folds of the posterior mucous (pg) and albumen (ag) glands. The small, pinkish cream, bulbous seminal vesicle (sv) overlies the end of the hermaphrodite duct within the albumen gland folds. This heavily folded, cream albumen gland is largely situated amongst the central folds of the paler posterior mucous gland. Single, very thin, short ducts join the seminal vesicle and the albumen gland to the junction of the hermaphrodite duct and start of the spermoviduct (sd). The long white translucent spermoviduct is initially wide, partially enveloped by the narrowing anterior mucous gland (am) and juxtaposed to an indistinct white prostate gland. The spermoviduct narrows and joins with the thinner bursal duct (bd) (joined by fine connective tissue of the duct wall) to pass through the outer posterior muscle stands of the anterior adductor muscle. Both ducts then pass, externally joined together by threads of connective tissue, between the adductor muscle and the foot wall to enter the small genital atrium (ga) close to the genital pore.

The spermoviduct enters dorsal to the bursal duct. Figure 4d indicates the duct openings into the genital atrium. Thick tissue folds occur in the lumen (l) in this atrium. The thin walled, brown bursa copulatrix (bc) appears deflated when not holding spermatophore, withering around a small mass of reproductive waste. Branching from the junction of the large, cream coloured epiphallus duct, is a long, thin, white flagellum (f). The shape of the pinkish cream lumen in the epiphallus duct is formed by a dominant fold (fig. 4g).

Hutton (1882a; pl. 15, fig. 2) and (1882b) (no figure) provides the only previous descriptions of *S. australis*, although only brief and incorrect in many details. Hubendick (1946; 49) incorrectly considered Hutton's anatomical descriptions of *S. australis* to apply to *S. "cookiana"*; Hubendick's generalized *S. "cookiana"* descriptions are actually of *S. australis* (1946; pl. 6, figs 20, 21, 22) agreeing with Knox (1955), who stated the genitalia of *S. "zelandica"* and *S. "cookiana"* are distinct, however, provided no comparative evidence.

Hubendick (1945:21, figs 21 and 26) and (1946: 14, fig. 12) apparently assumed the closeness of the spermoviduct and the bursal duct between the foot wall and the adductor muscle indicated they opened into a "vagina" before entering the genital atrium. Neither the "vagina" or an enclosed "stiletto-like copulation organ" (Hubendick, 1945:20-21; 1946:36) were found in any of the specimens dissected.

Spermatophore (fig. 4e)

In the bursa copulatrix between three and five spermatophore ($\bar{x} = 3.4$, $s = 0.8$, $n = 5$) are held, coiled in a brown gelatinous matrix. The spermatophore test is smooth, thin and transparent enclosing a white matrix. The blunt, cylindrical head is $50\text{--}60\text{ }\mu\text{m}$ in diameter and twice the length and thickness of the pointed tapering tail. A slight keel along the tapering region between the head and tail sections was observed on one specimen.

The spermatophore of *S. "australis"* was briefly described by Hutton (1882a) and Hubendick (1946).

Radula (pl. 6d, e, f)

The radula ribbon of *S. australis* exhibits the characteristic wide variation in dentition of siphonariids. In particular the number of lateral teeth and transverse rows varies greatly between individuals.

The mean dentition formula is 35:1:35 ($s = 7.01$, $n = 5$) with about 127 ($s = 7.33$, $n = 5$) anteriorly convex transverse rows. Of the 35 half row laterals, 20 ($s = 4.98$) are mid and 15 ($s = 3.58$) outer lateral teeth means respectively ($n = 5$). Inner laterals are absent. In each transverse row a gradual reduction in tooth size occurs from the inner mid laterals to the outer laterals on the ribbon fringe, with a corresponding increase in the width between transverse rows. The central tooth has a lower profile than the flanking mid laterals and a narrow pointed mesocone. The basal plate of the central tooth is about as long as that of the immediate flanking mid laterals and has a broad, blunt anterior fork and a posterior notch. The notch and fork provide interlocking articulation between rows. The broad basal plates of the inner mid laterals similarly interlock. The mid laterals possess a bluntly pointed mesocone and a broad pointed ectocone (pl. 6d, e). The ectocone is strong but protrudes at an acute angle halfway along the tooth's length. The mid lateral mesocones overlap the posterior of the corresponding mesocones of the row in front. The outer laterals typically have a basal plate about as broad as the tooth's length, supporting a "chisel" shaped pointed mesocone flanked by small, irregularly pointed, single ecto and endocones (pl. 6f). The angle of separation of each cone from the mesocone varies.

The radula formulae for this species of 36:1:36 ("*australis*") in Hutton (1882b) and repeated in Suter (1913), with 30:1:30 ("*australis*") and 35:1:35 ("*cookiana*") in Hubendick (1946; p. 49 and 36 respectively), are well within the variation limits presented here. However, the number of transverse rows, stated only in Hutton (1882b) (160) is above the variation presented.

Geographical Variation

Significant differences in shell morphology (table 1b) were found to occur between the seven population samples (table 3). No sufficiently large, recently collected sample of mature shells was available to include a comparison of southern South Island populations. High significant differences were found for shell length, width and height dimensions, length:width and width:height ratios ($p < 0.001$), while the length:height ratio and number of ribs were of a lower significance ($p < 0.01$). Comparative ordering of population samples indicated a wide intersample variation existed for most shell variables (0.05 prob. level). The number of shell ribs and the length:height ratio results indicated an overall similarity between samples, apart from the North Island samples from Whangamumu and Whangaparaoa which had a significantly larger number of ribs and length:width ratio respectively. The Chatham Ids sample had a overall larger shell than other populations sampled, particularly to the generally smaller shells from the proximal Pipikariti and N. Nelson population samples. The absence of aligned homogeneous groupings indicated the shell form was widely variable with shell variables exhibiting independant variation.

Compared to cogener shell measurements (table 4), the standard deviations of single shape dimensions for *S. australis* are generally lower while those for the quotient ratios are larger. These changes, along with the absence of aligned homogeneous groupings between population samples shows this species' shell form is extremely variable. Such variation suggests *S. australis* is an ecologically specialized species. Wide variation in shell form, particularly between rock and holdfast occurrences, also suggests a response to different environmental conditions.

Descriptions of Synonym Type Material

The type material of other species previously considered distinct, now considered synonyms of *S. australis*, are listed below.

Siphonaria radiata Blainville, 1827:194 *nomen dubium*

Types

Lost

Type Reference

Described in Dictionnaire des Sciences Naturelles, 41:294; figured only in Manuel de Malacologie et de Conchyliologie (plate volume) (pl. 2, figs 4, 4a).

Type Locality

Unknown.

Remarks

Hubendick (1946) synonymised this nominal species with *S. australis* without explanation or regard for priority. Although the original description appears to closely characterise *S. australis*, the original figure exhibits no such resemblance. As the types are lost (P. Bouchet, pers. comm), the original figure and description inadequate and no type locality nor distribution were indicated, *S. radiata* is regarded as a *nomen dubium*.

S. radiata Sowerby, 1835:6 (possibly a synonym of *S. pectinata* (Linne, 1758)) and *S. radiata* Adams and Reeve, 1850:69 (non 1848: auct.) (possibly a synonym of *S. japonica* (Donovan, 1834)) are primary homonyms of this nominal species.

To avoid confusion *Pileopsis radiata* Blainville, 1826 (Dictionnaire des Sciences Naturelles, 40: 462; unfigured) having a closely similar shell form, is mentioned as a secondary homonym. However, this name must be regarded as *nomen dubium* as the type specimens are missing (P. Bouchet, pers. comm.).

Siphonaria costata Hombron and Jacquinot, 1841: 192 *nomen nudum*

Types

Un sighted.

Type Locality

Otago ("Tavai-Pounamou"), New Zealand.

Remarks

This species is unfigured and the name is a primary homonym of and preoccupied by *S. costata* Sowerby, 1835 (type loc. Guacomayo, Central America).

Siphonaria inculta Gould, 1846: 153, pl. 30, fig. 464.

Types

Holotype, United States National Museum of Natural History, Smithsonian Institution (U.S.N.M.), 5857; Paratype (1), Museum of Comparative Zoology, Harvard (M.C.Z. 169190, ex. N.Y.S.M. 313)

Type Locality

New Zealand

Description of Holotype (pl. 3b)

Shell height slightly greater than 1/3 shell length; exterior extremely eroded; apex posteriorly offset to the left and dark brown; approximately 32 irregular radial ribs; siphonal ribs prominent; radial ribs on right of shell more prominent; interior glossy; cephalic muscle scar weakly convex; spatula and siphonal groove white to tan mottled with brown; adductor muscle scars deep and pale brown; shell margin greatly thickened and tan; shell lip tan with broad white rays aligned with exterior ribs.

Siphonaria cancer Reeve, 1856: species 7, pl. 2, figs 7a, b.

Types

(Herein designated) Lectotype (longest and widest syntype, most closely matches original figure) B.M. (N.H.) 198112; Paralectotypes (4) B.M.(N.H.) 198112.

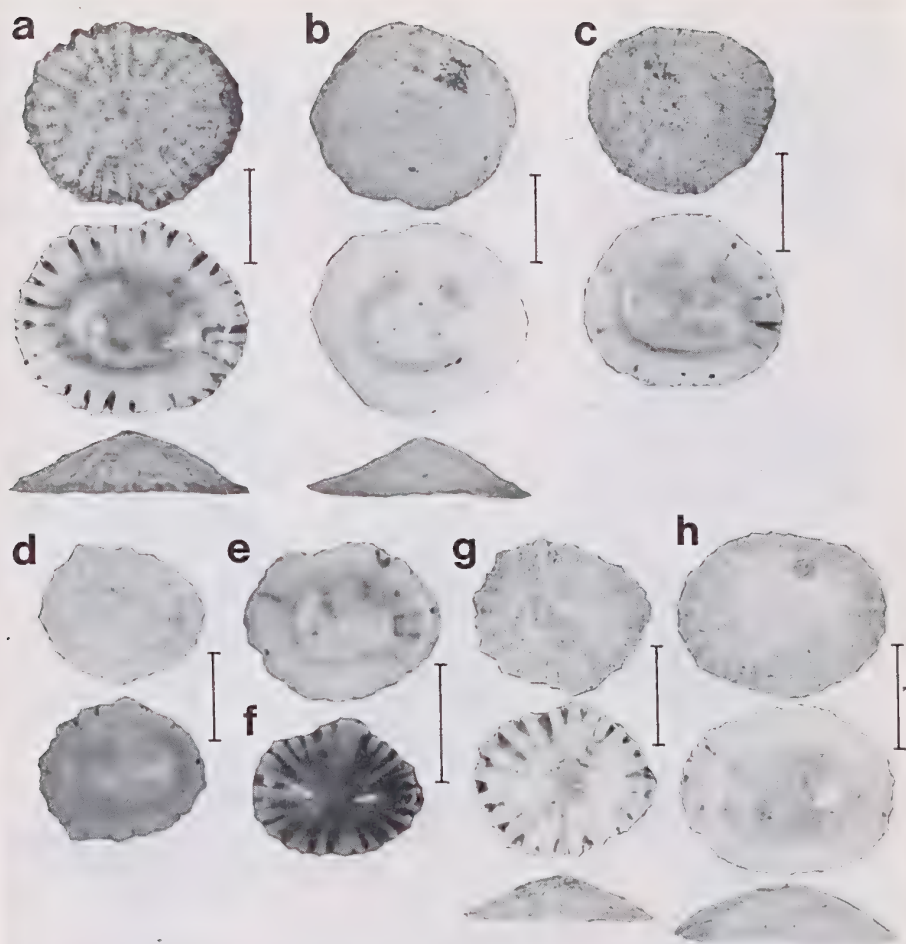


Plate 2. *Siphonaria zelandica*; a) Shelly Beach, rock platform, Caloundra, Qld. (repro. syst. fig. 3b; spermat. fig. 3d); b-c) Radar Reef, Rottnest Is, W. A. (repro. syst. for c fig. 3c); d) Streaky Bay, S. A. (repro. syst. fig. 3a); e) sea wall, Fremantle, W. A. f) Broome, N. W. A. g-h) *P. elegans* paratypes, Keppel Bay, Qld.; anterior of dorsal and ventral views aligned with right-hand side of plate, 1cm bar scale.

Type Locality

New Zealand

Descriptions of Lectotype (pl. 3c)

Shell height less than 1/3 shell length; apex strongly offset to posterior and left of shell; growth lines indistinct; apical sides convex; exterior greyish brown with darker rib interstices; approximately 36 irregular, strongly raised, radial ribs; siphonal ribs prominent and extend past shell lip; interior glossy; spatula whitish mottled with dark brown; adductor muscle scars prominent and pale tan; cephalic muscle scar weakly convex; shell margin thickened and dark tan with unequal pale tan to white rays aligned with exterior rib extremities.

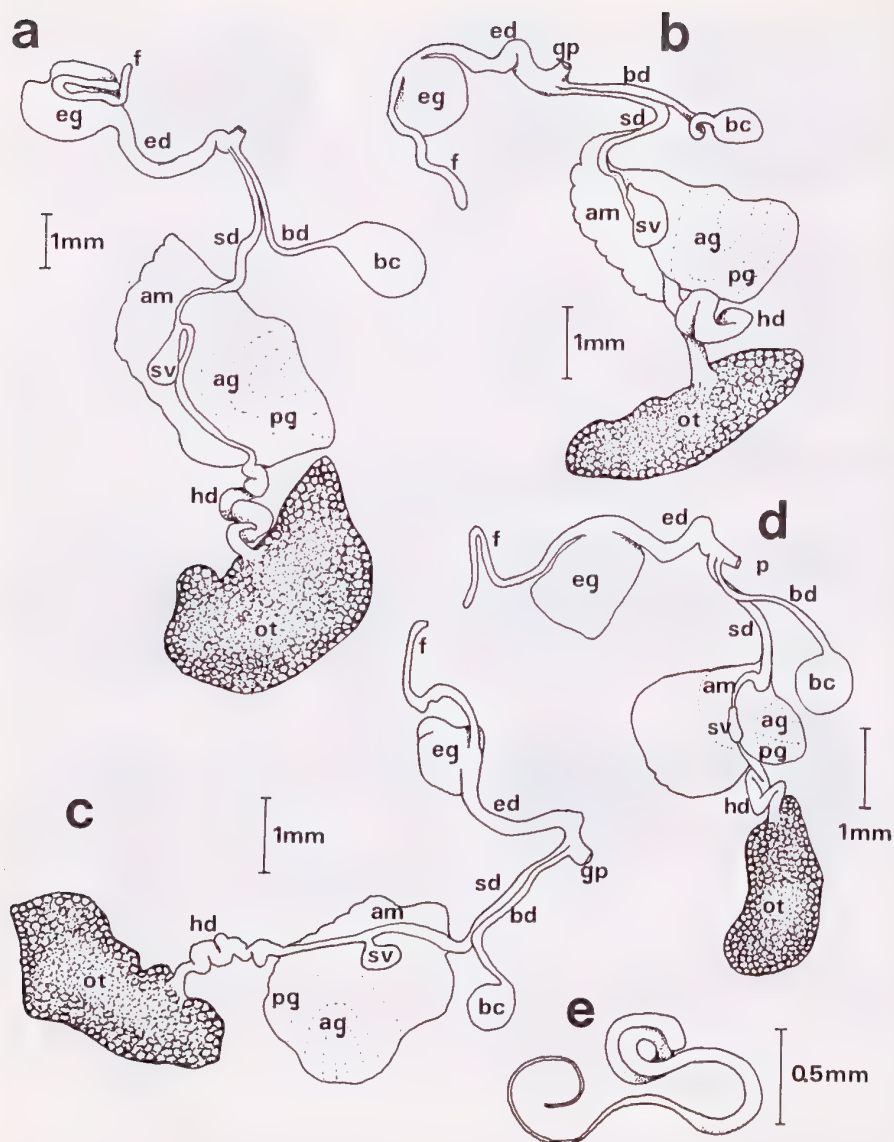


Fig. 5. Reproductive systems and spermatophore of *S. propria*. a) holotype (pl.5a) dorsal view; b) paratype (pl.5b) dorsal view; c) N. Arm of Port Pegasus, Stewart Is., N.Z. (pl.5d) dorsal view; d) Kare Kare, W. Coast, Auckland, N.Z. (pl.5f) dorsal view; e) spermatophore of holotype.

Abbreviations:

AO — accessory atrium, ag — albumen gland, am — anterior mucous gland, bc — bursa copulatrix, bd — bursal duct, ed — epiphallus duct, eg — epiphallus gland, f — flagellum, ga — genital atrium, gp — genital pore, hd — hermaphrodite duct, i — lumen, ot — ovotestis, pg — posterior mucous gland, sd — spermoviduct, sv — seminal vesicle.

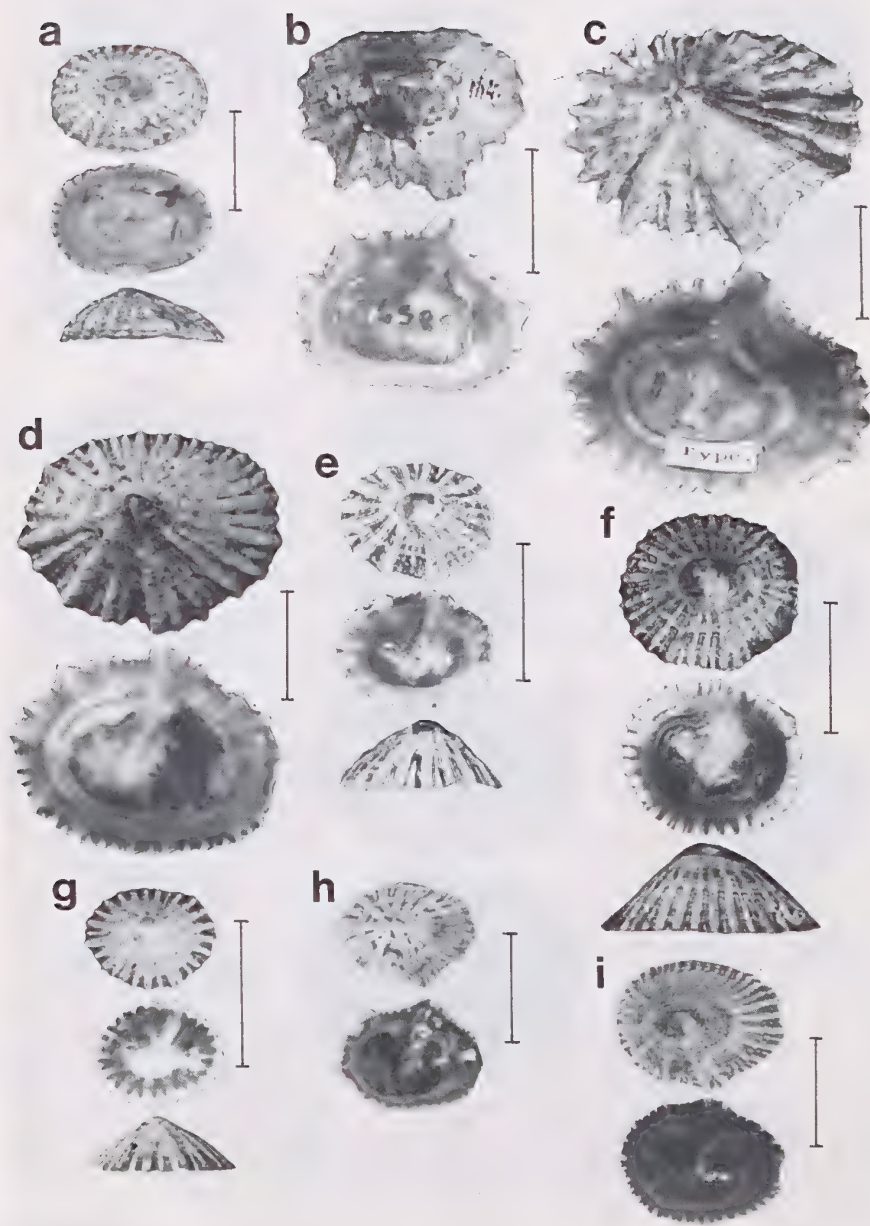


Plate 3. *Siphonaria australis*; a) lectotype (herein designated), Cook Strait; b) *S. inculta* holotype, New Zealand; c) *S. cancer* lectotype (herein designated), New Zealand; d) *S. cancer* paralectotype; e) *S. cookiana* lectotype; f-g) *S. cookiana* paralectotypes; h-i) Fossil Point, N. Nelson N.Z. (repro. syst. of h fig. 4a); anterior of dorsal and ventral views aligned with right-hand side of plate, 1cm bar scale.

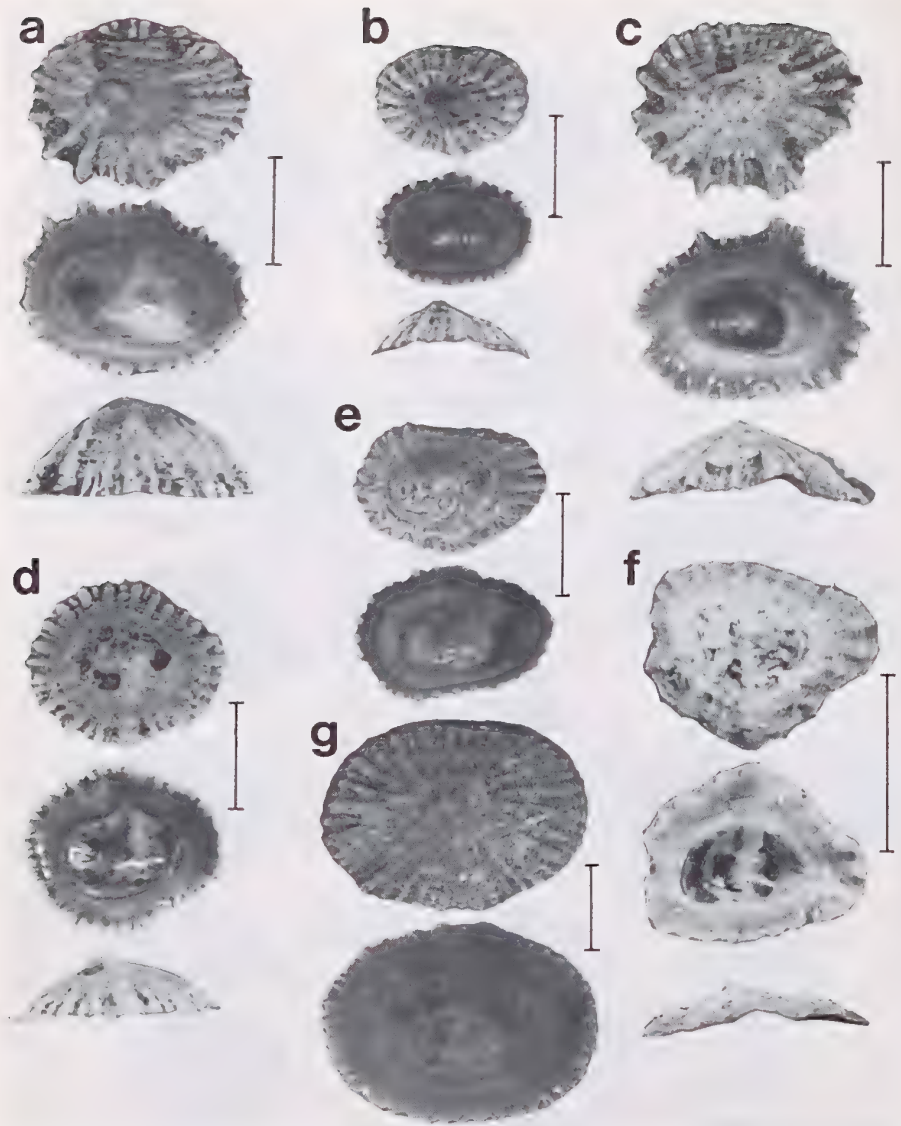


Plate 4. *Siphonaria australis*; a) Takapuna, N.E. of Auckland; b) Akau, near Whangamumu; c-d) Motutara, N. Is, N.Z. e) Fossil Point, N. Nelson, N.Z. f) Station Point, on *Durvillea*, Snares Ids (repro. syst. fig. 4b; spermat. fig. 4f); g) Port Waikato; anterior of dorsal and ventral views aligned with right-hand side of plate, 1cm bar scale. *Siphonaria cookiana* Suter, 1909: 258, pl. 11, fig. 18.

Types

(Subsequent designation; Boreham (1959) Lectotype, New Zealand Geological Survey (N.Z.G.S.) T.M. 1197; Paralectotypes (6); (1) A.M. C29118, not examined by Boreham (1959); (5) N.Z.G.S. T.M. 1198 —1202.

Type Locality

Lyall Bay, Cook Strait and Preservation Inlet, New Zealand.

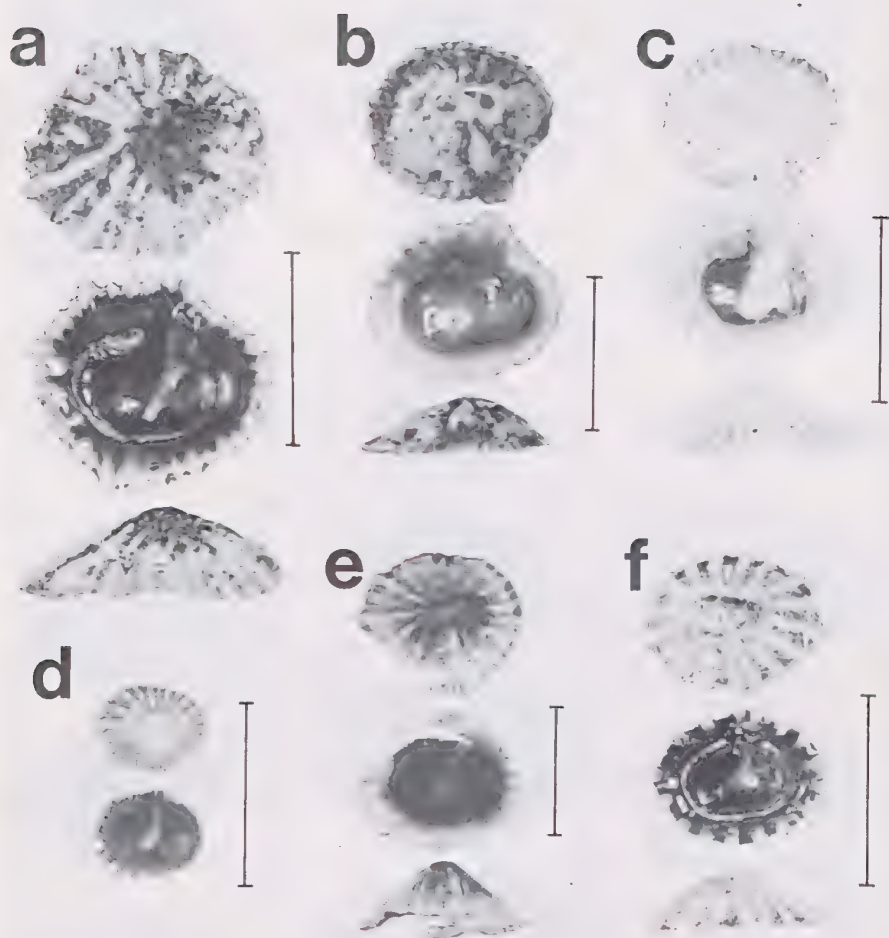


Plate 5. *Siphonaria propria* a) holotype, S. side of Kaikoura Peninsula, S. Is., N.Z. (repro. syst. fig. 5a; spermat. fig. 5e); b) paratype (repro. syst. fig. 5b); c) Fossil Point, N. Nelson; d) N. Arm, Port Pegasus, Stewart Is. (repro. syst. fig. 5c); e) Fossil Point, N. Nelson (broken shell); f) Kare Kare, W. coast of Auckland (repro. syst. fig. 5d); anterior of dorsal and ventral views aligned with right-hand side of plate, 1cm bar scale.

ADDITIONAL MATERIAL EXAMINED (PRESERVED (P) AND DRY (D))

New Zealand: Tiritiri Is, Hauraki Gulf (N.Z.G.S.) (1d); Takapuna, Auckland (N.Z.G.S.) (15+d); W. coast, Auckland; Motutara (N.Z.G.S.) (10d), Kare Kare, (1p); Taranaki (4d); Otakekohe, S. Taranaki (N.Z.G.S.) (15+d); Cook Strait, Wellington (3d); South Is; Fossil Pt, N. of Nelson (N.M.N.Z.) (15+p, 3d); S. side of Kaikoura Peninsula (15+p, 3d); Shag Pt, Otago (N.Z.G.S.) (2d); Preservation Inlet (topotypes) (N.Z.G.S. Suter colln.) (1d); North Arm, Port Pegasus, Stewart Is (N.M.N.Z.) (4p, 3d); total (35+p, 60+d).

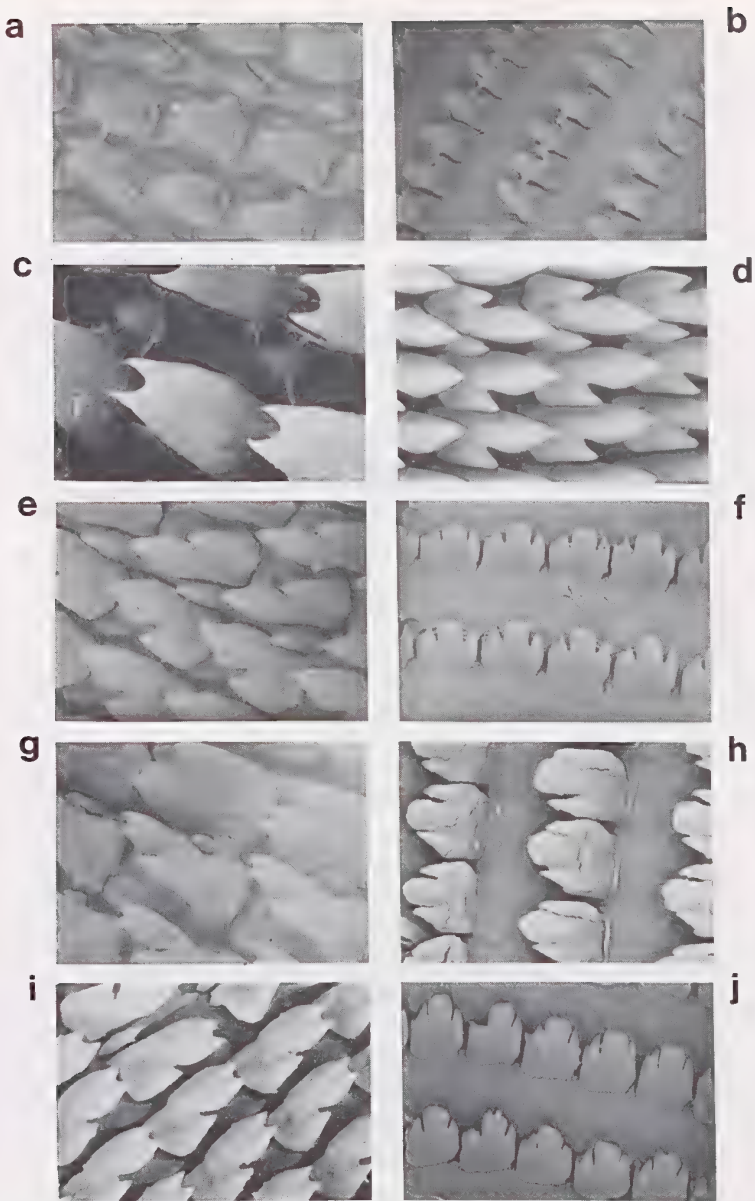


Plate 6. S.E.M. photomicrographs of radulae; a-c) *S.zelandica*; a) central and inner lateral teeth X 560 and b) mid and outer lateral teeth X 550, Radar Reef, Rottnest Is. W. A. SEM Stub 1126; c) central and inner lateral teeth X 650. Radar Reef, Rottnest Is. W. A. SEM stub 1154; d-f) *S.australis*; d) central and mid lateral teeth X 650, Station Point, Snares Ids, N.Z. SEM stub 1130; e) central and mid lateral teeth X 860 and f) outer lateral teeth X 860, Fossil Point, N. Nelson, N.Z. SEM stub 1129; g-j) *S.propria* sp.nov.; g) central and mid lateral teeth (note aberrant mid laterals) X 570 and h) outer lateral teeth X 1000, Fossil Point, N. Nelson, N.Z. SEM stub 1128; i) central and mid lateral teeth X 840 and j) outer lateral teeth X 570, Kare Kare, W coast of Auckland, N.Z. SEM stub 1127.

DISTRIBUTION

The known occurrence of this species is at lower littoral levels of mainly exposed rocky coasts throughout the North, South and Stewart Islands of New Zealand (fig. 2). Powell (1979) indicates this species also exists at the Chatham Islands. It is not recorded from the Bounty, Antipodes or Auckland Islands.

DESCRIPTION

External morphology (preserved animals)

The sole of the foot is broad, smooth and coloured cream to pale yellow. The side of the foot is smooth to weakly pustulose, superficially mottled with grey or black, with small unshaded circular spots aligned around pustules opening from subepithelial mucous cells. The edge of the foot is white and thin. The mantle is broad but thin, shaded grey with irregular black bands corresponding to shell rib interstices. Around the lobed and slightly swollen mantle edge is a continuous white to cream subepithelial band. Two small, subepithelial, black eye spots are centralized in the two thick, wide, cream cephalic folds which have a pale ventral edge. The tissue over the head and cephalic folds is superficially shaded black. The pneumostomal lobe is long, wide, white and weakly shaded with black mottling. The internal dorsal epithelium covering the visceral mass is tipped with black, concentrated over the siphonal duct and pallial cavity and decreasing in density over the buccal mass and ovotestis.

Shell (pl. 3f, g; 5a-i)

length mm $\bar{x}$ = 11.4, s = 1.54, n = 25

width mm $\bar{x}$ = 9.7, s = 1.32, n = 25

height mm $\bar{x}$ = 3.2, s = 0.67, n = 25

The shell is ovate, asymmetrical, posteriorly wide and relatively small with the apex slightly offset posteriorly and to the left. The apex is low, usually less than 1/3 the shell length and notched with a small protoconch. The pale brown exterior, often overgrown with algae or eroded, has about 30 (s = 4.7, n = 25) slightly raised and irregularly spaced, pale brown to white, rounded radial ribs. These ribs curve and broaden from the apex to overlap the shell lip. One or two secondary ribs may develop in the dark brown interstices between the apically continuous ribs. Rib widths range from broad to narrow. Apical sides are weakly convex. The fine radial growth lines are indistinct. Radial ribs extend past the shell lip relative to rib size. On the right of the shell, the two juxtaposed, prominently raised siphonal ribs project the farthest. The interior shell lip and margin are thickened. The glossy shell interior has a cream to tan spatula and siphonal canal with a purply brown to dark brown colouration around the spatula and in and below the narrow, deeply grooved muscle scar. The shell margin can be pale purple (pl. 3a) or dark brown (pl. 3d, e). External ribbing is reflected on the inner shell lip and margin by white shallow grooves tipped with brown interstitial rays. The deep siphonal groove is prominent, curving from the spatula to the shell lip. The cephalic muscle scar (fig 1C; cms) is narrow, shallow and posteriorly concave. As the shell matures, the ribs and interior margin thicken, the spatula colour darkens from a cream or tan to a dark purply brown while the shell lip changes from dark brown to a purply white (pl. 3a, b, adults; pl. 3d, f, subadults). The siphonal angle 0° is about 80° (s = 5.54, n = 10).

Reproductive system (fig. 5a, b, c, d)

The epiphallus duct (ed) and gland (eg) lie over the anterior buccal mass under the thin cuticle covering the visceral mass. The other major reproductive ducts and glands are situated in the right posterior region of the coelom, ventral and posterior to the large digestive gland and more anterior branchial cavity.

The yellow, granular ovotestis (ot) is situated in the most posterior area of the coelom (above the foot muscle tissue). Joined by several small, thin, translucent ducts to the ovotestis is the large, thin walled, pinkish cream section of the hermaphrodite duct (hd). This duct straightens and narrows to a thin transparent duct as it enters the enveloping folds of the posterior mucous (pg) gland. The cream folded albumen gland (ag) is centred

in the lateral folds of the white posterior mucous gland. A very small, translucent duct from the albumen gland along with a short, thin, white seminal duct join the narrow section of the hermaphrodite duct as it enters the thin walled spermoviduct (sd). The seminal vesicle (sv) is large bulbous and a pinkish white colouration. The white, translucent anterior mucous gland (am), and extension of the posterior mucous gland, extends along part of the short thickened lower section of the spermoviduct. An indistinct white prostate gland is juxtaposed to the anterior mucous gland and dorsal to the spermoviduct. The anterior edge of the anterior mucous gland is lobed. The bursa copulatrix (bc) is brown, spherical and thin walled, enclosing spermatophore in a gelatinous matrix. The lower spermoviduct and the long, thin, white bursal duct (bd) enter the small genital atrium closely connected by ductal tissue after passing through a few outer posterior stands of the anterior adductor muscle. The bursal duct is ventral to the slightly thicker spermoviduct. The genital pore (gp) is small. The narrow, cream to white epiphallus duct (ed) is long with internal lobes and folds in its thin wall. A long thin cream coloured flagellum (f) appears as an extension of the epiphallus duct from the joint of the duct with the large, bulbous, partially lobed, epiphallus gland (eg).

The reproductive system of *S. propria* was briefly described and figured by Hutton (1882b) as *S. "zelandica"*; indicated by the bicuspidate mesocone of the lateral teeth in the corresponding radula figure. Hubendick's (1945; 1946) description and figures of the reproductive system of *S. "cookiana"*, are really of *S. australis*.

Spermatophore (fig 5e).

In the bursa copulatrix between 1 and 4 spermatophore ($x = 2.3$, $s = 1.2$, $n = 6$) are tightly coiled in a brown gelatinous matrix. The spermatophore body consists of a blunt cylindrical head (50-60 μm in diameter) tapering to a thin, "thread" like, transparent tail. The thin, soft, transparent body test of the head section encloses a pinkish white gelatinous core which appears coiled. The tail section contains no core and is about $\frac{1}{4}$ of the total spermatophore length. In an animal 9.9 mm long a spermatophore was 4.5 mm long.

Radula (pl. 4g, h, i, j)

The number and shape of radula teeth and the number of transverse rows varies greatly between individuals. Teeth, particularly the mesocones, towards the front of the radula ribbon are usually worn and often broken.

The mean dentition formula is 21:1:21 ($s = 3.9$, $n = 6$) with about 108 weakly curved (anteriorly convex) transverse rows ($s = 10.9$, $n = 6$). Of the 21 half row laterals, 9 ($s = 2.6$) are mid and 12 ($s = 1.4$) are outer lateral teeth means respectively ($n = 6$). Inner lateral teeth, typically not possessing endo or ectocones, are absent. The central and first few flanking mid laterals articulate with the corresponding teeth in adjacent transverse rows. The separation between transverse rows increases to the outer extremities of the radula ribbon where outer laterals of different rows are separated by more than a tooth's width.

The central tooth has a lower profile than the flanking mid laterals and a pointed mesocone about half the tooth length, curving up from an elongated basal plate. This plate has a blunt, broad anterior fork and a blunt posterior notch, enabling aligned articulation between central teeth. Strongly branching at an acute angle from the outer side of each mid lateral tooth is a pointed ectocone. The mid lateral's mesocone is bicuspidate with the inner cusp longer than the outer. The cusps are separated by a shallow "U" to "V" shaped cleft (pl. 4g, i, j). The lateral's ectocone is often widely offset to the side of the mesocone but generally points directly forward. Aberrant laterals are common appearing as extremely broad teeth (pl. 4g; mid lateral). Outer laterals have a square basal plate supporting a broad, flat "chisel" like mesocone flanked by pointed single ecto and endocones. The widths and angles of separation of endo and ectocones are variable.

The radula for this species has been previously described only briefly by Hutton (1882b) ("*zelandica*" and repeated by Suter 1913). Both the number of teeth and rows recorded by Hutton (33-40:1:40-33 with 130-140 rows) are well above the variation limits presented here.

Geographical variation was not examined.

Etymology

From proprius, (Latin, = peculiar, special); referring to the special need to rename this species.

TAXONOMIC DISCUSSION

Descriptions of *S. zelandica* in Hutton (1878), Suter (1913), Powell (1939; 1946; 1957; 1979), Hubendick (1946), Knox (1955) and Morton and Miller (1968) refer to shell variants of *S. australis*.

S. baconi with pale, and *S. zebra* with dark, internal radial rays (corresponding with rib interstices), are shell forms of *S. zelandica*, both exhibiting the low conical shape, weakly subcentral apex, characteristic primary and secondary ribbing and shell colouration. T. Woods (1879) erroneously considered *S. baconi* to be a variant of *S. diemenensis*. The shell morphology (types examined) and reproductive system (McAlpine, 1952: 43, fig 2) of *S. diemenensis* is specifically different, particularly in shell ribbing, size of epiphallus gland and duct and the length of bursal and spermoviducts. Iredale (1924) considered *S. "bifurcata"* (really meant *S. zebra*) as the Peronian representative of the Western Australian *S. baconi*, however, provided no comparative evidence. Hubendick (1946) suggested *S. albida* Angas, 1867 in Tate and May (1902) (undescribed and unfigured) as a bibliographical synonym of *S. baconi*, however as *S. baconi* is not recorded from Tasmania, Tate and May's record probably refers to *Trimusculus conicus* (Angas, 1867) with which *S. albida* is synonymous (types examined). Further Hubendick (1946) suggested *S. baconi* may be conspecific with *S. bifurcata* and considered *S. zelandica* a synonym of *S. australis*. In the same monograph Hubendick also considered *S. elegans* and *S. baconi* distinct species and *S. zebra* synonymous with *S. kurracheensis* Reeve, 1856. Anatomical investigations and examination of types by McAlpine (1952) revealed that *S. elegans* was conchologically conspecific with the figure of *S. "bifurcata"*, but that the reproductive system he had dissected differed greatly from the genitalia of *S. "bifurcata"*, in Hubendick (1946). Hubendick (1955), after examining the types of the species in question, realized the anomaly indicating *S. "bifurcata"* in Hubendick (1946) was described from a mixed lot (N.M.V.F.13785, Port Jackson; has since been separated into species) and suggested that *S. elegans* and *S. zebra* are conspecific and synonyms of *S. zelandica*. Subsequent examination of the relevant type specimens and original descriptions indicates that the texts of *S. zebra* and *S. bifurcata* (not the figures) in Reeve's revision had been transposed (typographical error; *S. zebra* is actually species 22 with figure 21). *S. elegans* in Hubendick (1945; 1946) was described from one misidentified preserved specimen of *S. kurracheensis* from Timor (indicated by the radula dentition formula); an anomaly also corrected in Hubendick (1955). The dentition formula of *S. "bifurcata"* is actually from a specimen of *S. diemenensis* from the mixed Port Jackson lot. The types of *S. zebra* are undoubtedly (type label has the correct locality data), and those of *S. bifurcata* most probably, from Australia and the Philippines respectively.

Reeve (1856), in his revision of the genus *Siphonaria*, apparently neglected to examine existing type material and consequently described *S. cancer* from New Zealand, omitting to mention either *S. inculta* or *S. australis* and erroneously synonymizing *S. zelandica* with *S. siphon* Sowerby, 1824. Unfortunately the types of *S. siphon* are missing (K. Way; pers. comm.), but examination of the original description and figure (Sowerby, 1824: no. 21, pl. 143, fig. 1) indicates *S. siphon* has a low subcentral apex, approximately 42 even, primary ribs, few secondary ribs, 3-4 siphonal ribs extending past the shell margin, a wide siphonal groove and a strongly convex cephalic muscle scar. Hutton (1878) suggested *S. cancer* was a variant of *S. zelandica* with which Hutton incorrectly synonymized *S. scutellum* Deshayes, 1841 and disregarded *S. inculta* as the original description was uncited. *S. scutellum* (types examined) is a synonym of *S. obliquata* Sowerby, 1825, a relationship realized by Hutton (1882b) (correction attributed to von Martens). *S. obliquata* has a large elongate shell with a strongly subcentral apex, low bistriate radial ribbing exteriorly accentuated with tonal colour banding. Hutton (1880), based upon Reeve's inadequate descriptions, placed *S. zelandica* and *S. inculta* into the synonymy of *S. siphon* and suggested *S. cancer* was "probably" also conspecific. *S. australis* was considered a distinct

species. While in Hutton (1882b), based upon Cuming's identification of *S. cancer* from Formosa (Cuming, 1865: — Hutton, 1880), Hutton omitted *S. cancer* from the New Zealand siphonariid fauna. Hutton's (1882a) description of an *S. "australis"* reproductive system, although incorrect in many details (e.g. inclusion of a vas deferens), is probably that of *S. australis*, having long and very thin bursal and spermoviducts. Hubendick (1946) realizing Hutton's errors, considered Hutton's figure to be that of *S. cookiana*. The *S. zelandica* reproductive system (animal found on rocks) described by Hutton (1882b) is also of *S. australis*, indicated by the pointed mesocone referred to in his description of the radula (the absence of a vas deferens should also be noted). The types of *S. inculta* and *S. cancer* are a large, heavily ribbed form of *S. australis* similar to the *S. "zelandica"* form in Suter (1913: 600, pl. 24, fig. 6) and Powell (1979: 292, pl. 54, fig. 10). The types of *S. australis* appear to be immature, not having the heavy ribbing or thickening of the shell margin and lip of larger specimens. Both Hubendick (1946) and Powell (1979) correctly synonymized *S. cancer* with *S. australis*.

Examination of reproductive systems and radulae of animals with shells similar to the lectotypes and paralectotypes of *S. cookiana* designated by Boreham (1959), indicates a mixed type series exists. The lectotype (pl. 3e) is a juvenile of *S. australis* (pl. 3h, similar shell; pl. 6e, f, radula; fig. 4a, reproductive system) while the paralectotypes (pl. 3f, g) are a distinctly different species (pl. 5c, f, similar shells; pl. 6g-j, radula; figs 5c, d, reproductive system). Suter's inadequate original description and figure was considered by Boreham (1959) to be generalized. Determined by the designated lectotype, *S. cookiana* becomes a synonym of *S. australis*.

S. cheesemani Oliver, 1915, *Parellisiphon innocuus* Iredale, 1940 and *Mestosiphon lentulus* Iredale, 1940, respectively described from the Kermadec, Lord Howe and Norfolk Islands, are all considered incorrect synonyms of *S. cookiana* or *S. australis* in Hubendick (1946) (all types examined). *S. "australis"* in Hubendick (1955) (lot N.M.V.F.13924, Masthead Is, Qld.) refers to a pale variant of *S. atra* Quoy and Gaimard, 1833. Dissections of animals with similar shells to the lot Hubendick examined show the reproductive system to be conspecific to that of animals conchologically similar to the syntypes of *S. atra* (type loc. l'île de Vanikoro).

S. spinosa Reeve, 1856, mentioned in Hutton (1882b), is unmistakably a synonym of *S. aspera* Krauss, 1848 (S. Africa) and incorrectly described from New Zealand (types examined).

Specific Variation

S. zelandica is distinctly different and possibly even subgenerically separable from *S. australis* and *S. propria*, possessing a bulbous spermatophore, a prominently larger muscular epiphallus gland and duct; all important divisive subgeneric characters. However, their radulae are similar in form and all possess a prominent flagellum and are without an accessory atrium on the epiphallus duct.

The following specific comparisons concentrate on reproductive systems, considered more precise for species differentiation, and to a lesser extent on the intraspecifically variable shell and radular characters.

Six distinct cogeners overlap in distribution with *S. zelandica*; *S. diemenensis*, *S. funiculata* and *S. tasmanica*, distributionally limited to south-eastern Australia; *S. denticulata*, distributed around northern Australia, overlaps on the eastern and western coasts; *S. kurracheensis*, distributed through parts of the Indian Ocean, overlaps on the north-western coast; *S. atra*, widely distributed throughout the Indo Pacific is presently known to overlap only on the north-eastern coast.

The reproductive systems of *S. funiculata* and *S. tasmanica*, belonging to the subgenus *Liriola* Dall, 1870, have large muscular epiphallus ducts and accessory organs but no flagella (Jenkins, 1981:8, figs 3a, b — *S. funiculata*, 3c — *S. tasmanica*). Compared with *S. zelandica*, their shell forms are apically taller (small width:height and length:height ratios, table 4), with a greater number of flattened primary ribs (table 4). *S. kurracheensis* and *S.*

denticulata, with morphologically similar reproductive systems, are subgenerically separable from *S. zelandica* having an elongated, thin flagellum, long thin bursal, epiphallus, hermaphrodite and spermoviducts and an elongated muscular accessory atrium (McAlpine, 1952: 43, fig. 1). The pale shell of *S. kurracheensis*, while similar to that of *S. zelandica*, is apically taller with strongly convex apical sides, prominent siphonal ribs and thickened, raised radial ribbing (types examined). The shell of *S. denticulata* is apically low with prominent primary ribs, particularly siphonal. *S. denticulata* mainly differs from *S. kurracheensis* in reproductive morphology by possessing smaller epiphallus and albumen/mucous glands. The reproductive system of *S. diemenensis* (McAlpine, 1952: 43, fig. 2) differs by having a small, soft epiphallus duct and gland, no accessory atrium and very long bursal and spermoviducts, a morphology similar to *S. australis* and *S. propria*. The shell of *S. diemenensis* is apically low, heavily ribbed with dark rib interstices and interior (types examined). *S. atra* has a reproductive system similar to those of *S. kurracheensis* and *S. denticulata* with long, thin bursal and spermoviducts, a thin elongated flagellum and an elongated accessory atrium, but differs by having a thickened epiphallus duct. The shell of *S. atra* is apically low, thickened around the shell margin in mature specimens and with numerous even primary ribs with 3-4 prominent siphonal ribs.

The reproductive systems of *S. australis* and *S. propria* are particularly similar (figs. 4a, b, c, and 5a, b, c, d), separable mainly on the presence or absence of the scalloped edge of the anterior mucous gland (scalloped in *S. propria*) and the size of the seminal vesicle (sv of *S. australis* is generally larger). While the number of radula teeth appears to be of little taxonomic importance, the shape of the inner lateral's mesocone is an extremely important distinguishing character (pointed in *S. australis*, bicuspidate in *S. propria*). The shells of *S. australis* and *S. propria*, although exhibiting wide variation, are readily separated by their internal colouration, especially on the spatula and siphonal groove.

S. obliquata, distributed throughout the southern parts of New Zealand, is the only co-existing cogener with *S. australis* and *S. propria*. However, possessing an extremely large epiphallus duct and epiphallus gland, genital atrium and genital pore, and a strongly lobed hermaphrodite duct, *S. obliquata* is markedly different the shell being particularly large, more elongated and slightly taller with more numerous radial ribs than *S. australis* and *S. propria* (table 4).

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Table 2. Rank analyses of variance and order relationships for geographical population samples (9) of *S. zelandica* ($n = 20$).

shell variable	Kruskal-Wallis rank analysis test (non parametric)		Multiple comparison test		for the multiple comparison between regions, the signs > < indicate magnitudes of heterogeneous partitions, while equal signs indicate homogeneous groupings (0.05 prob. level).
	length	width	length:width	length:width:height	
primary ribs	79.74	80.10	42.01	13.06	
	36.19	36.19	36.19	2.81	
height	79.74	80.10	42.01	10.67	
	36.19	36.19	36.19	2.81	
length:height	79.74	80.10	42.01	13.06	
	36.19	36.19	36.19	2.81	
Single classification, two-tailed anova					
F ₃					
Fo.01 (9.171)					
significance	p < 0.001	p < 0.001	p < 0.001	p < 0.002	1 = 2 = 3 = 4 = 5 = 6 > 7 < 8 = 9
	not significant	p < 0.001	not significant	p < 0.002	1 = 2 = 3 = 4 = 5 = 6 < 7 = 8 = 9
Student-Newman-Keuls test					
significance	p < 0.001	p < 0.001	p < 0.001	p < 0.002	1 = 2 < 3 > 4 > 5 < 6 = 7 = 8 = 9
	not significant	p < 0.001	not significant	p < 0.002	1 = 2 < 3 > 4 > 5 < 6 = 7 = 8 = 9

Keppel Bay, Qld.
 Sydney, NSW.
 E. Vic.
 Port Phillip, Vic.
 E. SA.
 W. SA.
 E. WA.
 Fremantle, WA.
 Broome, WA.

